Crocodile in a Tree - An Exhibition on Evolution and Biodiversity

Scheyer, Torsten M ; Straehl, Fiona R ; Sánchez-Villagra, Marcelo R

Abstract: Evolution and tree-thinking, The origin of crocodylians, Fossil crocodylians from Urumaco, The group of modern crocodylians, Which information does body shape of a crocodylian convey? Form and function, in crocodylians, Biology of crocodylians (Breathing , Locomotion, Heart anatomy, Communication, Skin, Threat and protection, Distribution, Lifespan and reproduction, Diet), Overview of taxa on display, Behind the curtain - the models in the exhibition.

Crocodile in a Tree

T. M. Scheyer
F. R. Straehl
M. R. Sánchez-Villagra

Scidinge Hall

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Torsten M. Scheyer, Fiona R. Straehl, and Marcelo R. Sánchez-Villagra

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An Exhibition on Evolution and Biodiversity

Scidinge Hall Verlag
2015

Title page: Section of the illustration from Jorge Gonzalez (Argentina)
on the species-rich crocodylian fauna of the Upper Miocene of Urumaco. Full image in Fig. 9.

ISBN: 978-3-905923-20-9

www.scidinge-hall-verlag.de

www.pim.uzh.ch
10 CHF / 9,50 €

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PREFACE

The public rarely has up-to-date knowledge about evolution. The media and internet misrepresent many aspects of the pattern and the mode of evolution. Creation of a new, special exhibition based on current understanding on the evolutionary history of crocodylians and their ancestors shall help to address this. Museums are ideal sites to convey scientific topics in an accessible fashion. By means of the evolutionary history of crocodylians, we present an example of the transformation of biodiversity in time and space. The displayed objects include three dimensional models of new palaeontological finds as well as fossils from various regions of the world, including Switzerland. When producing these objects, access for people with visual impairment was an important consideration, one that we expect will enhance the quality of the exhibition for all visitors. The focus lies on the extraordinary diversity of skull shape and body size in relation to the ecology of extant crocodylians as well as their ancestors in the deep geological time. The shape of a tree is used as an analogy to illustrate the branching process of evolutionary diversification in contrast to a single, linear 'ancestor-descendent' succession. The exhibition also contributes to make valuable objects from the collections of the Zoological and Palaeontological Museum of the University of Zurich accessible to a broader public. We wish all the visitors a pleasant experience in the exhibition "Das Krokodil im Baum" ("Crocodile in a tree").

Torsten Scheyer, Fiona Straehl, &
Marcelo Sánchez-Villagra

EVOLUTION AND TREE-THINKING

The diversity of life is one of the most obvious things about the Earth. Living in the city, surrounded by buildings, this might not seem obvious. As we go to a park, the suburbs, or a forest, many novel plants, animals and fungi may become apparent. These only make up the part of the diversity visible to the naked eye. This diversity is comprised of the number of species and forms. In addition, the shape and size of organisms are different. When comparing organisms we also see that they exhibit many similarities. In biology, creatures are grouped by means of such similarities. The theory of evolution explains why organisms can be grouped according to resemblances: they have common ancestors. It also explains why living beings are in fact diverse. Animals, plants, fungi and bacteria all change as time passes, over decades, centuries, millennia and millions of years. This knowledge was established by comparisons among recent organisms and with observations on domesticated plants and animals. Later comparisons to fossils helped to document these transitions.

The diversity of life makes sense only when one recognizes that organisms have acquired their form and function through evolution. The way to understand – to put order - to the diversity of life is through phylogeny, best represented in an evolutionary tree. An evolutionary tree shows the history of evolution and how organisms changed over time. All living species had a common ancestor, the descendants of which branched off over time, thereby yielding a tree-like pattern.[1] Phylogenies are obtained by anatomical comparisons, molecular data and through information from the fossil record. Fossils provide evidence for the type of creatures that lived at a specific time in the past. In addition, they are a direct record of extinction, a dominant characteristic of evolution. Where the fossil record is well preserved, it shows that typical species survive for up to few millions of years and disappear afterwards. In some cas-

[1] The same is true for human evolution. A common misunderstanding is that humans are direct ancestors of chimpanzees. In reality, chimps are not our ancestors; we only share a common ancestor. Some descendants of this ancestor have evolved into chimps, others led to the hominid lineage.

es, this happens when a new species has evolved from the more basal species. Many branches of the evolutionary tree of all living beings, however, are dead ends. It is estimated that 99% of all species that ever evolved have become extinct.

The terrestrial environment changes constantly. Lowlands turn into mountain ranges, seas desiccate and turn into deserts, jungles develop on previously frozen grounds. Such processes, in addition to less dramatic changes in environmental conditions, influence the evolution of organisms.

Evolution is accepted as a fact in science; it is obvious that descent with modification took place in space and time. It is not controversial. Evolution is a matter of fact just like planet earth rotates around the sun. The mechanisms underlying the origin, modification and splitting-up of species - how evolution functions - are still under investigation. It is not surprising that such a complex matter involves several mechanisms.

Many people directly associate evolution with natural selection, an important aspect of evolution discovered by Charles Darwin and Alfred Russel Wallace. The success of different variations of organisms and consequently the genes that are passed on to the next generation largely depends on environmental factors. If these factors remain constant, natural selection favors stasis. Changing environmental conditions lead to strong selection pressure, which favors specific variations of organisms to the disfavor of others. Accordingly, evolutionary change can occur rapidly.[2] The metaphor of "survival of the fittest" implies a struggle for life and potentially leads to the misconception that evolution is a struggle of each against everyone; this is wrong. Instead, cooperation and symbiosis play a key role in biological systems.

Besides natural and sexual selection, which is evoked by competition for mates of the other sex within a species, evolution is driven by other mechanisms. For example genetic drift. It may happen that

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Fig. 1. Evolutionary tree of life (illustration by Tara Gschwend, SIVI UZH; schematic drawings of organisms by Beat Scheffold, PIMUZ). See legend on the following double page.

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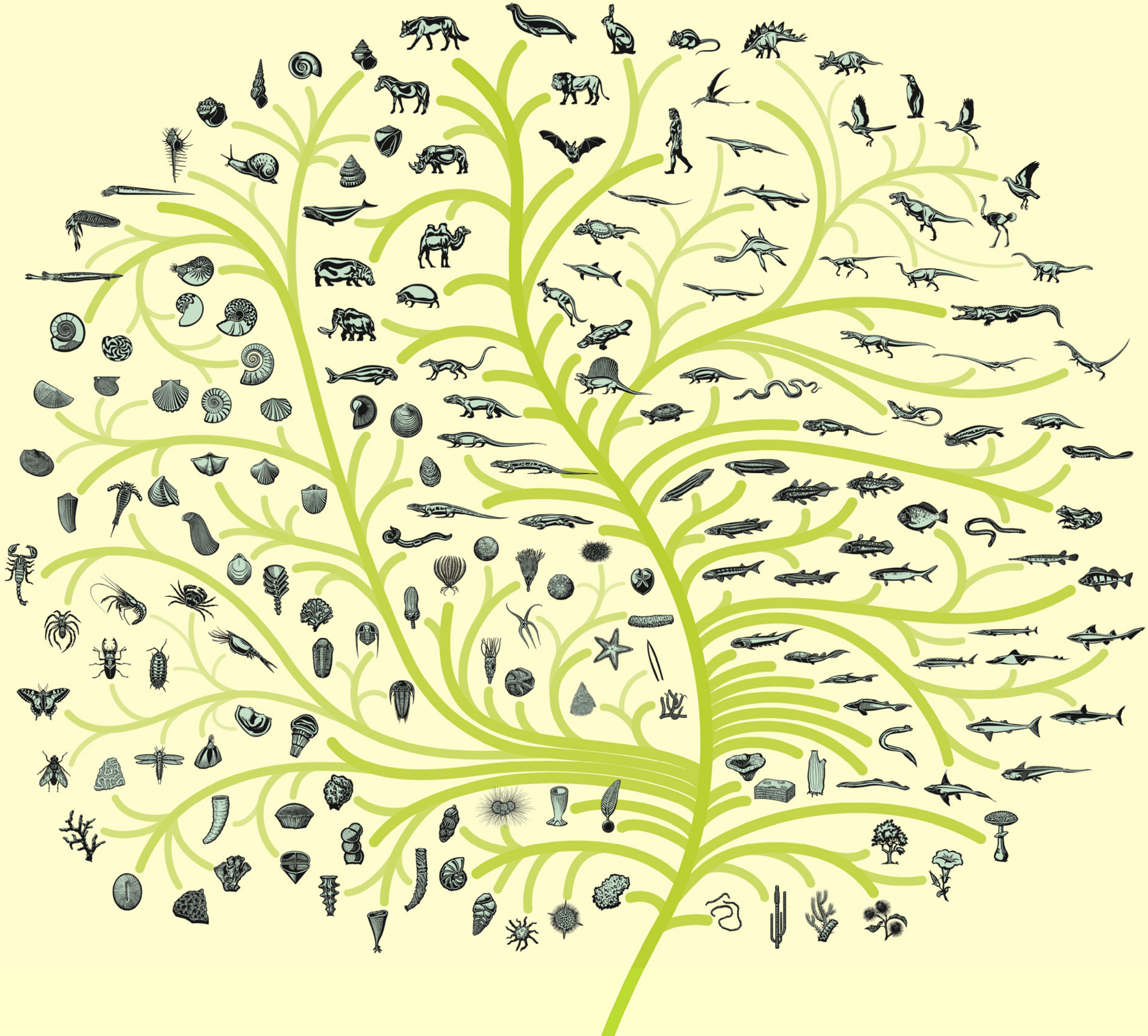
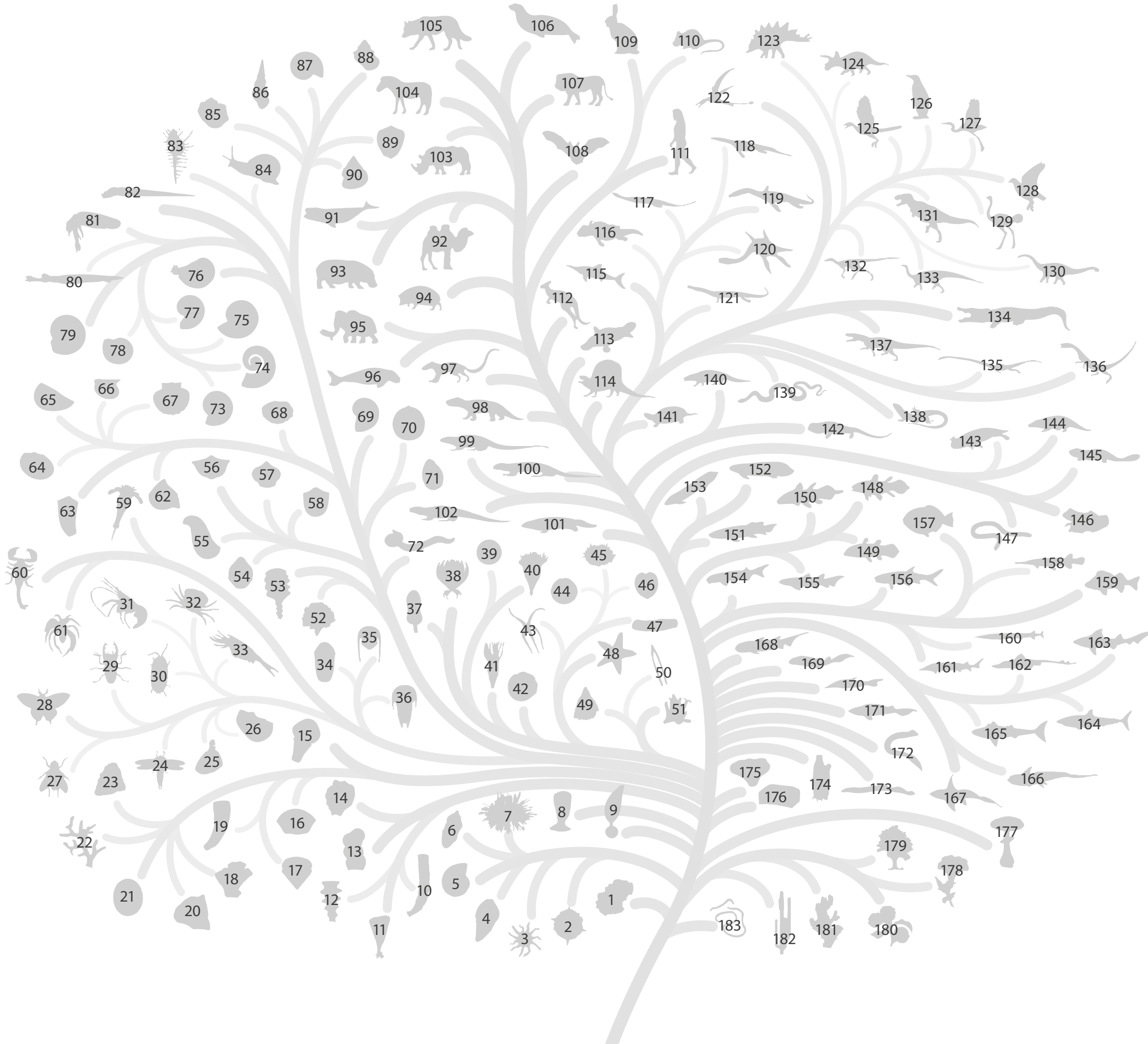
[2] The most famous example for this possibly is the drastic change in the appearance of the peppered moth in industrial areas in Great Britain at the end of the 19th century. The bark of local birches turned dark due to contamination of the air by soot. The typical light colouring of the peppered moth did not camouflage the moths in those areas anymore. Individuals with dark colouring therefore had an advantage over the lighter varieties since they were well camouflaged on the birches. Eventually, darker individuals dominated peppered moth populations.



No.	Taxon	English Name	Occurence	No.	Taxon	English Name	Occurence	No.	Taxon	English Name	Occurence
1	ARCHAEA	Archaea	Quarternary-Precambrian	62	*Trigonia*	clam	Jurassic-Cretaceous	123	*Stegosaurus*	dinosaur	Jurassic
2	*Hexacontium*	Radiolaria	Quarternary	63	*Hippurites*	rudist (bivalve)	Cretaceous	124	*Triceratops*	dinosaur	Cretaceous
3	*Astrorhiza*	foraminifera	Quarternary-Palaeogene	64	*Posidonia*	clam	Carboniferous	125	*Archaeopteryx*	early bird	Jurassic
4	*Textularia*	foraminifera	Quarternary-Cretaceous	65	*Daonella*	clam	Triassic	126	*Aptenodytes*	great penguin	Quarternary-Neogene
5	*Lenticulina*	foraminifera	Quarternary-Jurassic	66	*Pterinea*	clam	Ordovician-Devonian	127	*Ardea*	heron	Quarternary-Neogene
6	*Uvigerina*	foraminifera	Quarternary-Carboniferous	67	*Pecten*	scallop	Quarternary-Eocene	128	*Columba*	pigeon	Quarternary-Neogene
7	*Globigerina*	foraminifera	Quarternary-Ordovician	68	*Buchiola*	clam	Devonian	129	*Struthio*	ostrich	Quarternary-Neogene
8	*Ajacicyathus*	sponge	Cambrian	69	*Bellerophon*	sea snail	Cambrian-Triassic	130	*Diplodocus*	dinosaur	Jurassic
9	*Charniodiscus*	Ediacaran fossil	Precambrian	70	*Neopilina*	monoplacophoran	Quarternary	131	*Tyrannosaurus*	dinosaur	Cretaceous
10	*Euplectella*	Venus's flower basket	Quarternary	71	*Tryblidium*	monoplacophoran	Ordovician-Silurian	132	*Lagosuchus*	dinosauromorph	Triassic
11	*Ventriculites*	glass sponge	Cretaceous (Jurassic, Palaeogene)	72	*Lumbricus*	earthworm	Quarternary	133	*Plateosaurus*	dinosaur	Triassic
12	*Hydnoceras*	glass sponge	Devonian	73	*Arietites*	ammonoid	Jurassic	134	*Crocodylus*	crocodile	Quarternary-Neogene
13	*Colospongia*	demosponge	Triassic (Permian, Carboniferous)	74	*Crioceratites*	ammonoid	Cretaceous	135	*Tanystropheus*	longnecked reptile	Triassic
14	*Spongia*	bath sponge	Quarternary	75	*Ceratites*	ammonoid	Triassic	136	*Macrocnemus*	reptile	Triassic
15	*Rhizostoma*	barrel jellyfish	Quarternary	76	*Nautilus*	nautilus	Quarternary-Palaeogene	137	*Ticinosuchus*	reptile	Triassic
16	*Favosites*	tabulate coral	Ordovician-Permian	77	*Cyclolobus*	ammonoid	Permian	138	*Lacerta*	lizard	Quarternary-Neogene
17	*Calceola*	slipper coral	Devonian	78	*Goniatites*	ammonoid	Carboniferous	139	*Natrix*	grass snake	Quarternary-Neogene
18	*Thecosmilia*	stone coral	Jurassic, Triassic, Cretaceous	79	*Anarcestes*	ammonoid	Devonian	140	*Seymouria*	reptilomorph	Permian
19	*Streptelasma*	horn coral	Ordovician-Devonian	80	*Passaloteuthis*	belemnite	Jurassic	141	*Emys*	pond turtle	Quarternary-Neogene
20	*Isastraea*	stone coral	Cretaceous-Jurassic	81	*Sepia*	cuttlefish	Quarternary-Neogene	142	*Discosauriscus*	reptilomorph	Permian
21	*Cyclolites*	stone coral	Cretaceous	82	*Orthoceras*	nautiloid	Ordovician-Triassic?	143	*Gerothorax*	amphibian	Triassic
22	*Corallium*	precious coral	Quarternary (-Cretaceous)	83	*Murex*	Venus comb	Quarternary-Palaeogene	144	*Eryops*	amphibian	Permian
23	*Platygyra*	stony coral	Quarternary-Palaeogene	84	*Helix*	Roman snail	Quarternary	145	*Andrias*	giant salamander	Quarternary-Neogene
24	*Stenodictya*	winged insect	Carboniferous	85	*Trachynerita*	snail	Triassic	146	*Rana*	frog	Quarternary
25	*Balanus*	barnacle	Quarternary-Palaeogene	86	*Loxonema*	snail	Ordovician-Triassic	147	*Typhlonectes*	Cayenne caecilian	Quarternary
26	*Mitrobeyrichia*	seed shrimp	Silurian	87	*Euomphalus*	snail	Silurian-Permian	148	*Latimeria*	coelacanth	Quarternary
27	*Musca*	fly	Quarternary	88	*Worthenia*	snail	Devonian-Triassic	149	*Macropoma*	coelacanth	Cretaceous
28	*Papilio*	swallowtail	Quarternary	89	*Trochactaeon*	snail	Cretaceous	150	*Diplurus*	coelacanth	Triassic
29	*Lucanus*	stag beetle	Quarternary	90	*Pleurotomaria*	snail	Jurassic-Cretaceous	151	*Dipterus*	lungfish	Devonian
30	*Porcellio*	woodlouse	Quarternary	91	*Balaena*	bowhead whale	Quarternary	152	*Uronemus*	lungfish	Carboniferous
31	*Aeger*	prawn	Triassic-Cretaceous	92	*Camelus*	camel	Quarternary-Neogene	153	*Neoceratodus*	Australian lungfish	Quarternary (-Jurassic?)
32	*Cancer*	crab	Quarternary-Palaeogene	93	*Hippopotamus*	hippopotamus	Quarternary-Neogene	154	*Cheirolepis*	ray-finned fish	Devonian
33	*Nahecaris*	crustacean	Devonian	94	*Erinaceus*	hedgehog	Quarternary	155	*Osteolepis*	lobe-finned fish	Devonian
34	*Phacops*	trilobite	Devonian (-Silurian?)	95	*Mammuthus*	mammoth	Quarternary-Neogene	156	*Palaeoniscus*	ray-finned fish	Permian
35	*Trinucleus*	trilobite	Ordovician	96	*Dugong*	dugong	Quarternary-Neogene	157	*Dapedium*	ray-finned fish	Jurassic-Triassic
36	*Paradoxides*	trilobite	Cambrian	97	*Henkelotherium*	early mammal	Jurassic	158	*Lepisosteus*	gar	Quarternary
37	*Encrinus*	feather star	Triassic	98	*Cynognathus*	therapsid	Triassic	159	*Perca*	perch	Quarternary
38	*Antedon*	feather star	Quarternary (-Jurassic?)	99	*Bruktererpeton*	four-footed vertebrate	Carboniferous	160	*Saurichthys*	ray-finned fish	Triassic
39	*Glyptosphaerites*	echinoderm	Ordovician	100	*Hylonomus*	reptile	Carboniferous	161	*Acipenser*	sturgeon	Quarternary
40	*Orophocrinus*	blastoid echinoderm	Carboniferous (Devonian?)	101	*Ichthyostega*	early land vertebrate	Devonian	162	*Raja*	ray	Quarternary
41	*Macrocystella*	cistoid echinoderm	Ordovician	102	*Gephyrostegus*	land vertebrate	Carboniferous	163	*Hybodus*	shark	Cretaceous-Triassic
42	*Edrioaster*	echinoderm	Ordovician	103	*Rhinoceros*	rhinoceros	Quarternary-Neogene	164	*Carcharodon*	shark	Quarternary
43	*Furcaster*	brittle star	Devonian-Silurian	104	*Equus*	horse	Quarternary	165	*Cladoselache*	shark	Devonian
44	*Plegiocidaris*	pencil urchin	Jurassic-Cretaceous	105	*Canis*	wolf	Quarternary	166	*Chimaera*	chimaera	Quarternary
45	*Sphaerechinus*	sea urchin	Quarternary-Neogene	106	*Phoca*	earless seal	Quarternary	167	*Ischyodus*	chimaera	Jurassic-Palaeogene
46	*Micraster*	heart urchin	Cretaceous	107	*Panthera*	lion	Quarternary-Neogene	168	*Climatius*	spiny shark	Devonian (-Silurian?)
47	*Thelenota*	prickly redfish	Quarternary	108	*Myotis*	mouse-eared bat	Quarternary	169	*Bothriolepis*	armour-plated fish	Devonian
48	*Asterias*	starfish	Quarternary-Neogene?	109	*Lepus*	hare	Quarternary	170	*Pteraspis*	jawless fish	Devonian
49	*Dictyonema*	graptolite	Cambrian-Silurian	110	*Mus*	mouse	Quarternary-Neogene	171	*Hemicyclaspis*	jawless fish	Devonian
50	*Didymograptus*	graptolite	Ordovician	111	*Homo*	human	Quarternary-Neogene	172	*Promissum*	conodont	Ordovician
51	*Rhapdopleura*	graptolite	Quarternary	112	*Macropus*	kangaroo	Quarternary	173	*Petromyzon*	lamprey	Quarternary
52	*Hippodiplosia*	moss animal	Quarternary	113	*Ornithorhynchus*	platypus	Quarternary	174	*Halocynthia*	red sea squirt	Quarternary
53	*Archimedes*	moss animal	Permian	114	*Dimetrodon*	early synapsid	Permian	175	*Elasmostoma*	calcareous sponge	Jurassic (Permian?-Palaeogene)
54	*Terebratula*	lamp shell	Quarternary-Neogene	115	*Ichthyosaurus*	ichthyosaur	Jurassic	176	*Stromatopora*	sponge	Silurian (Ordovician-Jurassic?)
55	*Productus*	lamp shell	Carboniferous-Permian	116	*Cyamodus*	placodont	Triassic	177	*Amanita*	fly amanita	Quarternary
56	*Cyrtospirifer*	lamp shell	Devonian	117	*Neusticosaurus*	marine reptile	Triassic	178	*Convolvulus*	bindweed	Quarternary (-Neogene?)
57	*Lacunosella*	lamp shell	Jurassic-Cretaceous	118	*Ceresiosaurus*	marine reptile	Triassic	179	*Acer*	maple	Quarternary-Palaeogene
58	*Orthis*	lamp shell	Ordovician-Permian	119	*Nothosaurus*	marine reptile	Triassic	180	*Arctium*	burdock	Quarternary-Neogene
59	*Eurypterus*	sea scorpion	Ordovician-Permian	120	*Plesiosaurus*	marine reptile	Jurassic	181	*Equisetites*	horsetail	Triassic
60	*Scorpio*	scorpion	Quarternary	121	*Askeptosaurus*	marine reptile	Triassic	182	*Voltzia*	conifer	Triassic
61	*Protolycosa*	spider	Carboniferous	122	*Rhamphorhynchus*	pterosaur	Jurassic	183	EUBACTERIA	eubacteria	Quarternary-Precambrian



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one gene variant accumulates randomly, especially in small populations where this effect is stronger. Genetic drift has been shown to be an important evolutionary mechanism.

In order to understand how evolution works, mechanisms responsible for the development of different variants of an organism have to be taken into account, including developmental biology and genetics. One example is the timing of developmental programs such as the differentiation of organs, which is controlled genetically or 'epigenetically', the latter meaning not simply ruled by DNA sequence. Changes in this process may involve morphological transformations that cannot be explained by ecology or population genetics alone.

It is important to realize that living beings are not optimal machines but rather the product of trade-offs evoked by their evolutionary history. Animals, plants and bacteria are not necessarily improving over time - they simply change. The reason for this lies in the historicity of the organisms. Evolutionary processes act on the available 'material' – thus on the groups of creatures, various shapes and sizes existing at a specific point in time and it acts on mutations present in these creatures. Changes within an organism can be interpreted as some kind of 'playing around' or 'managing' the available 'material', which is the result of the previous evolutionary history of the organism.[3] Each alteration and each new feature in an organism is based on modification of existing structures. Generations are able to survive if their features are merely 'sufficient' and not only if they are perfect.

Living beings are always a mosaic of ancestral and derived characteristics. Evolution can thus not be regarded as some type of ladder where a new group of animal or plant is present on every rung - a common misconception in humans. Neither does evolution have a goal, running from more 'primitive' to more complex life forms. On the other hand, it is not completely random. Evolution is a complex and highly dynamic process, not always happening at the same speed. Furthermore, such a complex matter is investigated intensively, by documenting the biodiversity that exists and existed in the past and the mechanisms that led to it.

[3] The French biologist François Jacob wrote a famous essay in 1977 in which he introduced the notion of tinkering or bricolage to a wide audience. The rearrangement and recombination of existing elements is a phenomenon that is common in evolution.

THE ORIGIN OF CROCODYLIANS

… or the transition from "crocodylian-like" (Crocodylomorpha) to modern crocodylians (Crocodylia).

In the exhibition, the common term 'crocodiles' is used to refer to what specialists would call '**crocodylians**', which is derived from the scientific name of the clade **Crocodylia** (gr. Κρόκη = gravel; δρῖλος = worm). The crocodylians not only include the true crocodiles such as the Nile- or Saltwater crocodile but also the alligators, caimans, and gharials.

Crocodylians from the Mesozoic and Cenozoic have been found on all the continents except for Antarctica, amounting to a rich fossil record for the group. Famous examples include one of the largest crocodylians *Sarcosuchus imperator* from the Cretaceous of Africa, as well as the widely distributed *Diplocynodon,* which has a fossil record of over one hundred specimens from Palaeogene and Neogene sites. New fossils from extinct species are described annually. In 2013 there were 16 species described, including the broad snouted caiman ***Globidentosuchus brachyrostris*** displayed in the **Diorama** and on the **large laboratory table**.

The early evolutionary history of crocodylians is well documented. The three groups of Crocodylia all include living crocodiles and make up the crown, and together with their extinct close relatives, called stem group representatives, they form **Crocodylomorpha**. These animals did not have much in common with Crocodyla. The earliest representatives of the Crocodylomorpha were the **sphenosuchians** (gr. σφηνος/ Sphenos = 'wedge' and Σοῦχος /Suchos = as a reference for *Sobek*, ancient Egyptian divinity depicted with crocodile skull). ***Dromicosuchus grallator*** in the **"tree of life"** belongs to this group. It was a small, agile predator from the Triassic and Jurassic.

Crocodylomorpha in turn are part of the **pseudosuchians** ("false corcodilians"), one of the two main lineages within the **archosuchians** ("ruler reptiles"). The other branch includes the extinct pterosaurs and

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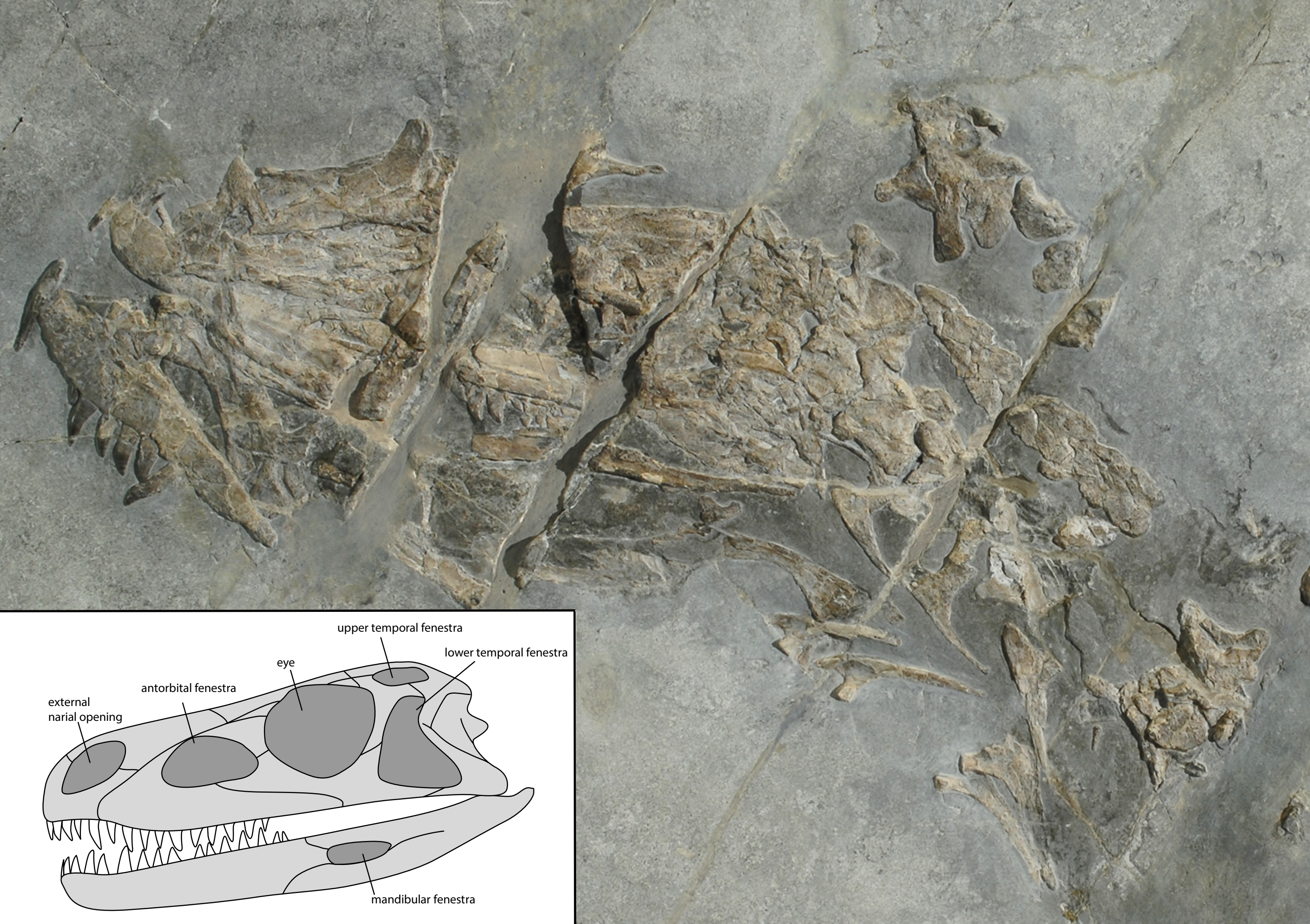
Fig. 2. The holotype skull (skull and part of trunk skeleton) of *Dromicosuchus grallator* in the North Carolina State Museum of Natural Sciences, Raleigh, NC, USA. The skull has a length of approximately 15 cm; the complete animal would have been a little over 1 m long.

Fig. 3-4. The fossil slab (holotype) of *Ticinosuchus ferox* at the Palaeontological Museum and the animal's life reconstruction by Beat Scheffold (PIMUZ). The animal had a total length of 2.50 m.

dinosaurs as well as modern birds. These two main branches split already during the Triassic (252 – 200 million years ago). Within the lineage of modern crocodylians, there are other more or less Crocodylomorpha-like groups, such as the heavily armoured **aetosaurs** or the **rauisuchians**. ***Ticinosuchus ferox*** (→ **"tree of life"**) falls within this lineage, it is a mid-Triassic top predator from the tropics. Most specimens of this species were found in the fossil-rich layer of the Besano formation of the World Heritage natural site of Monte San Giorgio. The large original plate containing ***Ticinosuchus*** is displayed in the **permanent exhibition** of the Palaeontological Museum. Crocodylomorpha are the only representatives of pseudosuchians to survive the mass extinction at the Triassic-Jurassic boundary (approximately 202 million years ago).

Similar to snakes and birds, the crocodylian skull has two temporal fenestrae. Turtles on the other hand do not have any temporal fenestrae and the last common ancestor of mammals, including humans, had only one. The basal archosaur skull is characterised by an additional opening, the antorbital fenestra right in front of the orbita, as visible on the ***Ticinosuchus*** skull. In modern crocodylians, the opening was closed secondarily and is therefore not identifiable.

Fig. 5. Close-up of the head of *Ticinosuchus* accompanied by an interpretative drawing (modified after Sen, 2005, based on Krebs, 1965). The skull is about 30 cm long.


upper temporal fenestra
lower temporal fenestra
eye
antorbital fenestra
external
narial opening
mandibular fenestra

FOSSIL CROCODYLIANS FROM URUMACO (→ DIORAMA)

A plethora of crocodylians inhabited northern Venezuela 5 million years ago. Until now, about 15 caiman- and gharial-like animals have been described scientifically. In certain regions there were up to seven species living in sympatry, meaning together in the same habitat, including swamps and a river delta. Nowadays, there are not more than two or at most three species inhabiting certain regions of the world simultaneously. The unusually high diversity of crocodylians in Venezuela was only possible since the individual species were specialised for different food, exploited different parts of the habitat, or had different temporal activity patterns – they were occupying different niches. This specialization is particularly noticeable in the large diversity of skull shapes. Additionally the range of size and mass was huge in the fossil forms. The smaller species, such as ***Globidentosuchus*** (→ **diorama, lab tables**), weighed relatively few kilograms and were between one and two meters in size. The larger species, such as the gigantic ***Purussaurus*** (→ **diorama, lab tables**) could reach a

Fig. 7. Schematic map of northern South America in which the most important fossil localities of Neogene age are marked.

Fig. 6. The fossil-rich Badlands of Urumaco in Venezuela.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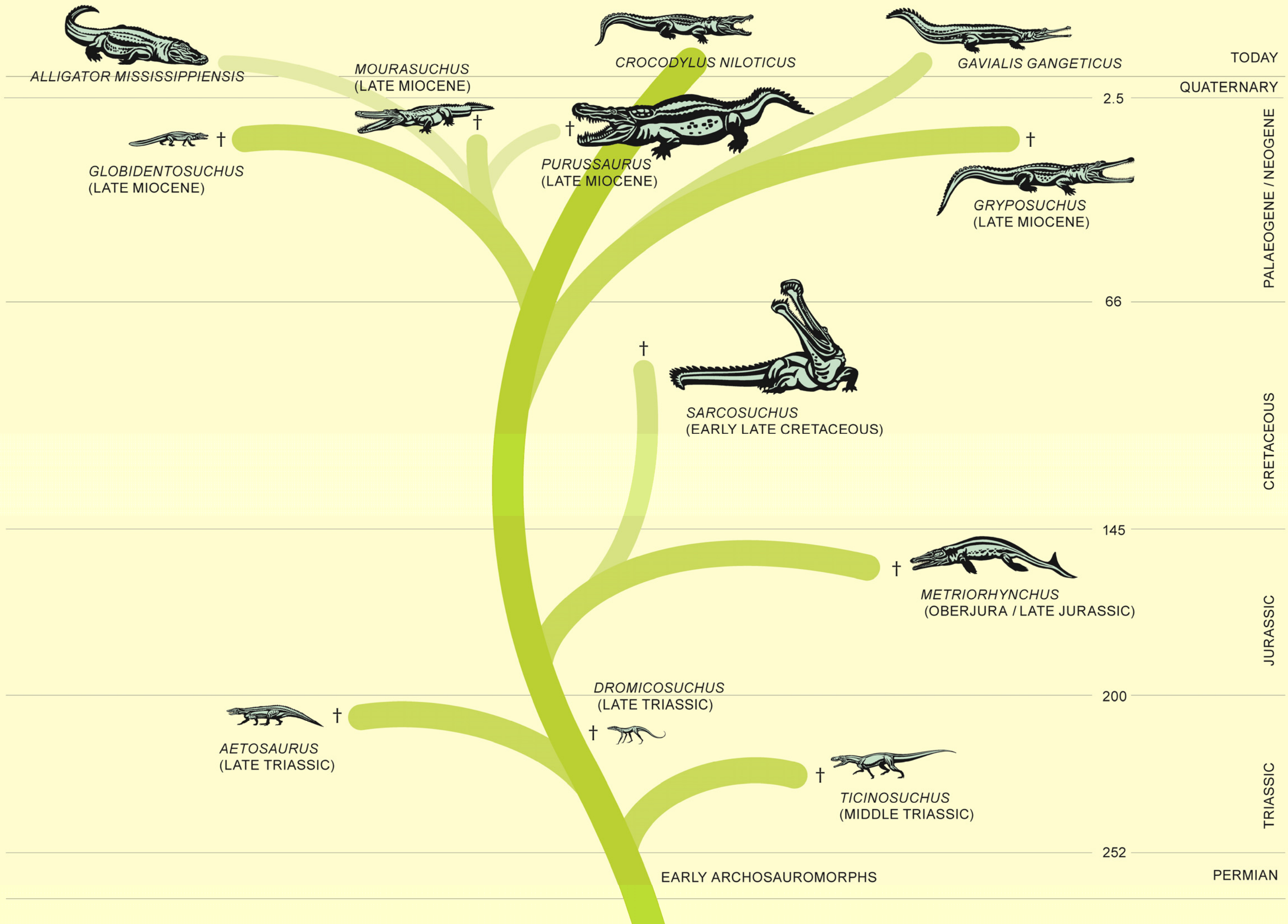
size of more than ten meters and a weight of several tons. ***Gryposuchus*** (→ **diorama, small lab table**), a carnivorous gharial, also measured up to ten meters, although it was not as massive as ***Purussaurus***. All these crocodylians lived in the South American tropics simultaneously.

Fig. 8. (previous double page). Illustration of the Upper Miocene crocodylian habitat, for example a wooded riverine environment, with some of the prey animals shown (illustration by Jorge Gonzalez, Argentina).

Fig. 9. Illustration of the species-rich crocodylian fauna of the Upper Miocene of Urumaco (illustration by Jorge Gonzalez, Argentina).


JORGE A. GONZALEZ
2013


ALLIGATOR MISSISSIPPIENSIS
MOURASUCHUS
(LATE MIOCENE)
CROCODYLUS NILOTICUS
GAVIALIS GANGETICUS
TODAY
QUATERNARY
2.5
GLOBIDENTOSUCHUS
(LATE MIOCENE)
PURUSSAURUS
(LATE MIOCENE)
GRYPOSUCHUS
(LATE MIOCENE)
PALAEOGENE / NEOGENE
66
SARCOSUCHUS
(EARLY LATE CRETACEOUS)
CRETACEOUS
145
METRIORHYNCHUS
(OBERJURA / LATE JURASSIC)
JURASSIC
DROMICOSUCHUS
(LATE TRIASSIC)
200
AETOSAURUS
(LATE TRIASSIC)
TICINOSUCHUS
(MIDDLE TRIASSIC)
TRIASSIC
252
EARLY ARCHOSAUROMORPHS
PERMIAN

THE GROUP OF MODERN CROCODYLIANS

Traditionally modern crocodylians are subdivided into three large groups, the crown groups: true crocodiles (**Crocodylidae**), the alligators (**Alligatoridae**) and the gharials (**Gavialidae**). Nowadays there are 15 crocodile species, eight alligator and caiman species, and just one gharial species. One skull representing of each of these groups is displayed on the large lab table: the Australian saltwater crocodile (***Crocodylus porosus***), the North American alligator (***Alligator mississippiensis***) and the Indian gharial (***Gavialis gangeticus***). The division into these three groups already took place at the end of the lower Cretaceous approximately 100 million years ago- a time where dinosaurs still populated the earth and pterosaurs flew in the skies.

Within the Crocodylia the representatives of the **Alligatoridae** and the **Crocodylidae** are classified as **Brevirostres** ("short snouted"), a group supported by morphological data.

All of the recent crocodylians spend time both in water and on land, they build their nests, lay their eggs, and bathe in the sun close to the riverside while they mostly catch prey in water. During their evolution, some crocodylian lineages did not lead an amphibian lifestyle. ***Dromicosuchus grallator*** (→ **"tree of life"**), for instance, lived fully on land. *Dromicosuchus* belonged to the **sphenosuchians**, a group of small, fragile crocodylomorphs with long legs - the second part of the species name *grallator* means 'stilt runner'. The displayed part of its skeleton was found in the upper Triassic of North Carolina in the USA, and was described in 2003. This 1.2 to 1.3 meter long individual was found right next to another larger predator, a close relative of ***Ticinosuchus*** (→ **"Tree of life", permanent exhibition** in the Palaeontological Museum), and it exhibits bite marks from this larger predator. On the other hand, **marine crocodylians** (thalattosuchians) from the Jurassic and Cre-

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Fig. 10. Crocodylian tree of life (illustration by Tara Gschwend, SIVIC UZH; schematic drawings of the animals by Beat Scheffold, PIMUZ).

taceous were well adapted to an oceanic lifestyle where they fed on molluscs and fish. The displayed skull of ***Metriorhynchus superciliosus*** (→ **large lab table**) from the Jurassic of southern England is one such thalattosuchian.

WHICH INFORMATION DOES BODY SHAPE OF A CROCODYLIAN CONVEY?

Science not only deals with the diversity of body structures of recent organisms but also with explaining their function. This discipline is called **functional morphology**. It is evident that shape and function are closely related, certain body structures enable an animal to lead a specific lifestyle.

Recent living beings are modified descendants and close relatives of other species. The specific body structure of a vertebrate can therefore only be the result of historic transitions. These transitions can be linked to behaviour or to adaptation to external circumstances. In order to understand the function of a specific body structure, knowledge about biomechanics, physiology, ecology, and behavioural biology are necessary. In palaeontology, direct data on physiology, ecology, and behavioural biology are often missing when investigating extinct taxa. Palaeontologists therefore try to reconstruct the biology and lineage of extinct vertebrates using the remaining structures that can be observed, usually only teeth and bone.

Due to their density and hardness, teeth and bones are better conserved than soft tissues and often are the only indicator of form and lifestyle of extinct vertebrates. Comparison to recent relatives allows for statements on size, locomotion, and even on physiology of extinct vertebrates.

The vertebrate skeleton not only serves as internal support, it also plays an important functional role concerning posture and locomotion. Most muscles attach to bones and leave traces in the form of rough patches and scars. In the skull, the cranial nerves run through apertures whose size and abundance convey information on the distribution and dimension of these nerves. In addition, the imprints of blood vessels are visible on the bone. The shape of the ends of the bones of the limbs provide evidence for the maximal rotation and swivelling movements and, together with muscle attachment sites visible on the bone, allow for conclusions on locomotion of vertebrates. Moreover, the skeleton constantly adjusts to changing stress and strain, which leads to modulations in bone structure visible to the naked eye.

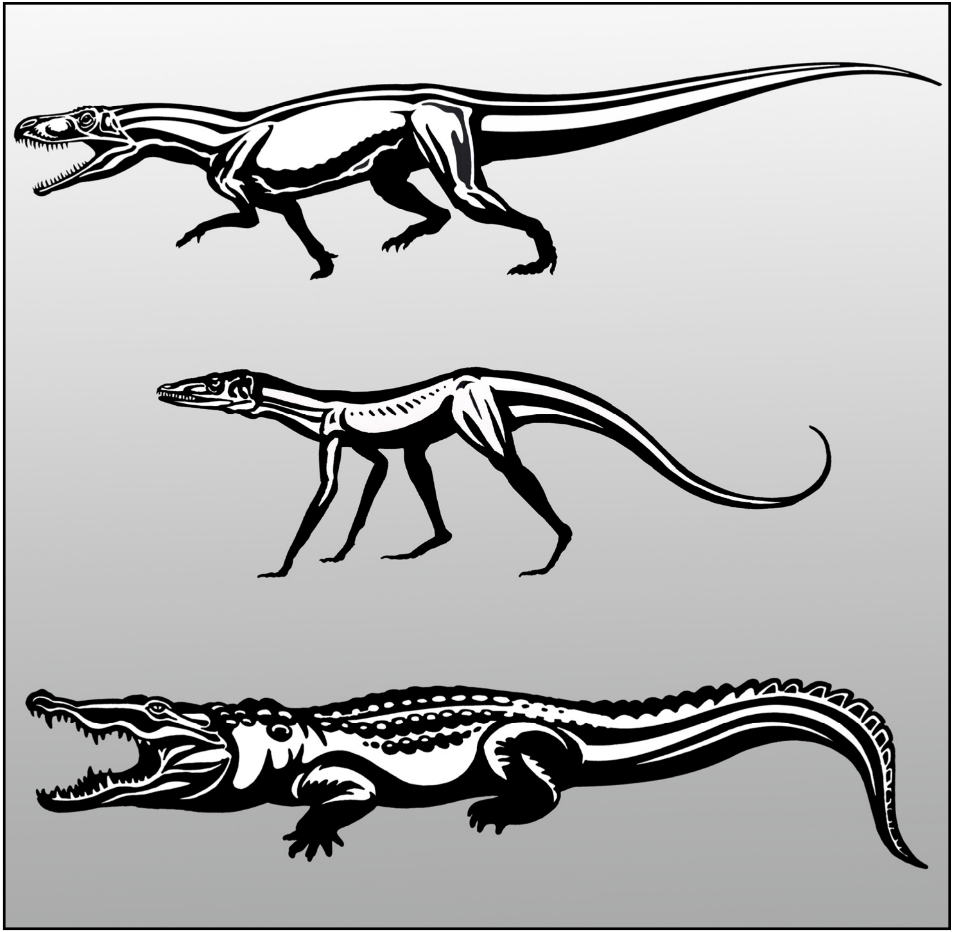


Fig. 11. Schematic illustrations of the Middle Triassic rauisuchian *Ticinosuchus* (above) and the Upper Triassic crocodylomorph *Dromicosuchus* (middle), which held their legs below the body - in comparison to the extant Nile crocodile (below) in (semi-erect) sprawling gait posture (schematic drawings by Beat Scheffold, PIMUZ).

FORM UND FUNCTION IN CROCODYLIANS (→ FILM „FORM AND FUNCTION“)

As in all other animals, form and function of the body in crocodylians is closely related. Fossils shed light on how the shape of structures changed during the course of evolution within the lineage leading to recent crocodylians. One example is provided by the comparison between the **Nile crocodile** (→ **lab tables**) and ***Ticinosuchus*** (→ **“Tree of life”, permanent exhibition** in the Palaeontological Museum). ***Ticinosuchus*** belongs to the rauisuchians, which together with the crocodiles, the dinosaurs and the pterosaurs are part of the Archosauria. The complete skeleton of ***Tichinosuchus*** on display in the Palaeontological Museum is the only one of this species and was it found in the Triassic rock layers of Monte San Giorgio in Tessin- where ***Ticinosuchus*** lived approximately 242 million years ago. The skeleton features relatively large legs placed on the ventral side of the body, which enabled the animal to perform what is called ‘real striding’, a type of gait also observed in mammals. This is supported by the straight shape of the femur and is further confirmed by fossil footprints of similar age found in Wallis, Switzerland. The femur of the **Nile crocodile** on the other hand is s-shaped and differs from ***Ticinosuchus’*** by its articular surfaces. Recent crocodylians exhibit a posture in which the legs are bent away from the body and are held and moved in a push-up-like position. Crocodylians spend most of their time in water, in contrast to the purely terrestrial ***Ticinosuchus***. They ca, however, place their legs underneath their bodies on land and are therefore able to walk upright at a slow pace.

The kind of habitat in which an animal lives, be it terrestrial or semi-aquatic, influences its diet, which in turn has an impact on the shape of certain structures within the body. Jaw and tooth shape are often the only indicators of feeding habits in extinct species. Two main feeding types already existed early in the evolution of crocodylians. Many groups have a tendency towards slender, elongated snouts, which are interpreted as linked with a water-oriented lifestyle. The **Indian gharial** (*Gavialis gangeticus*) (→ **large lab table**), which lives in the Ganges River, is an impressive example of such a specialised crocodylian. Its slender jaw- with more than 100 perfectly interlocking teeth- is comparable to the jaw of dolphins. Oth-

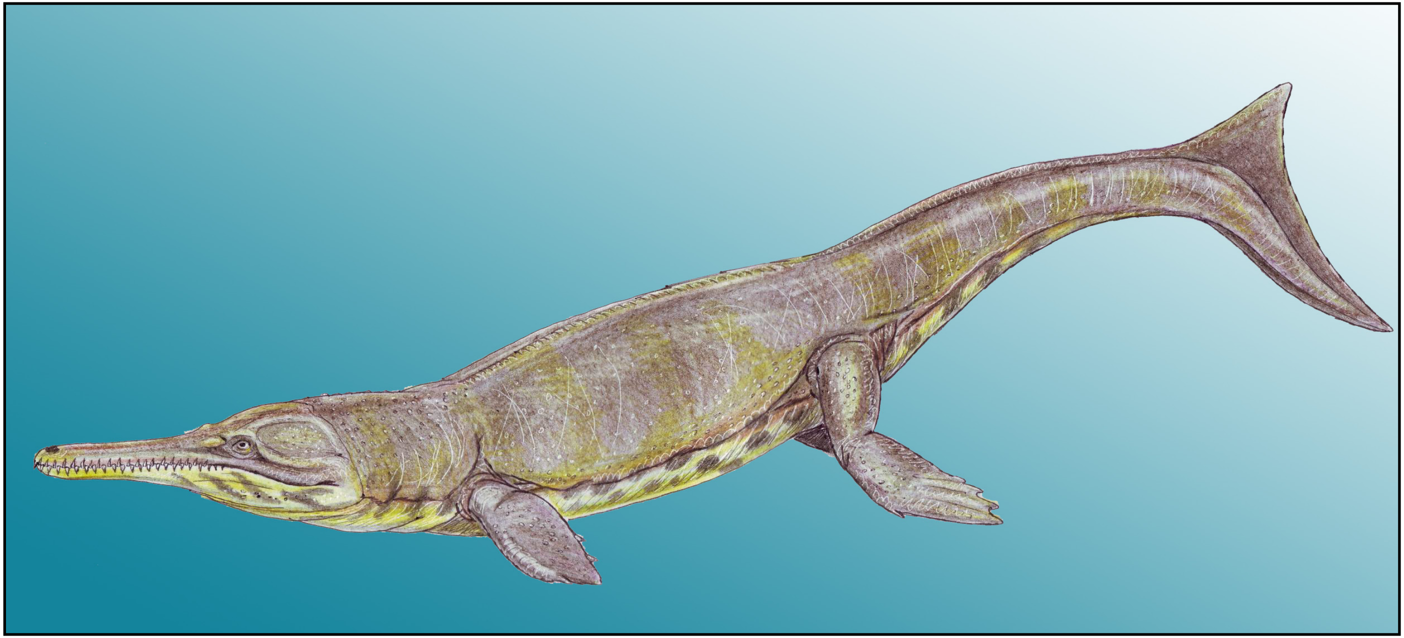


Fig. 12. Drawing of life reconstruction of *Metriorhynchus superciliosus* (copyright Dmitry Bogdanov, Licene CC BY 3.0, Wikipedia; background modified).

ers specializations are recorded in obligate aquatic marine crocodiles from the Mesozoic (Jurassic and Cretaceous), which exhibit paddle-like legs and a caudal fin. One representative of this group is ***Metriorhynchus superciliosus,*** whose skull and lower jaw are displayed on the **large lab tables**. However, at this time there were also groups of terrestrial crocodylians with tall and narrow snouts and laterally flat-

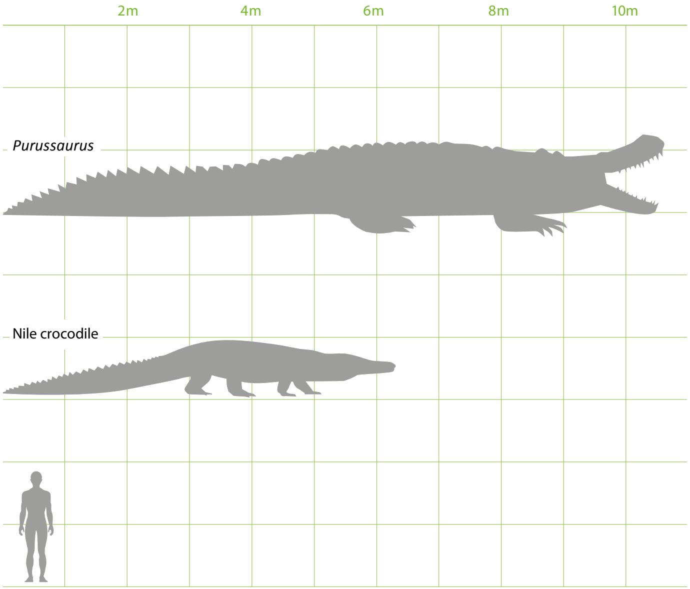


Fig. 13. Comparison of the body size of a human with that of a Nile crocodile and *Purussaurus* (illustration by Tara Gschwend, SIVIC UZH).

tened teeth with sawing edges, similar to those of carnivorous dinosaurs. After the extinction of dinosaurs such crocodylians were the most successful and predominant group of terrestrial predators.

Broad snouts, as in recent alligators and caimans, are characterised by their high bite force made possible by huge jaw adductors that are arranged under the skull so the animals can submerge more in water. The **saltwater- or estuarine crocodile** (***Crocodylus porosus***) (→ **large lab table**), the largest living crocodylian, has the highest bite force measured so far, at 16'460 Newton. This force approximately equals the weight force of a mid-range car. The bite force of large predators like lions or tigers, ranging around 4'450 Newton, is significantly lower. Bite force correlates with body weight, therefore extinct crocodylians including the caiman ***Purussaurus***) (→ **diorama, lab tables**) are estimated to reach a bite force of 69'039 Newton based on their body length of 12.5 meters and their weight calculated thereof. This even exceeds the bite force assumed for *Tyrannosaurus rex*!

Slender jaws lack the attachment sites for large jaw adductor muscles; therefore, mainly fish-eating crocodylians such as the **Indian gharial** do not have a large bite force. Their snouts are optimised for abrupt and precise movements in water and rapid opening and closing - they face less water resistance due to small surface area. Feeding on fish, as well as small reptiles and amphibians, does not require a high bite

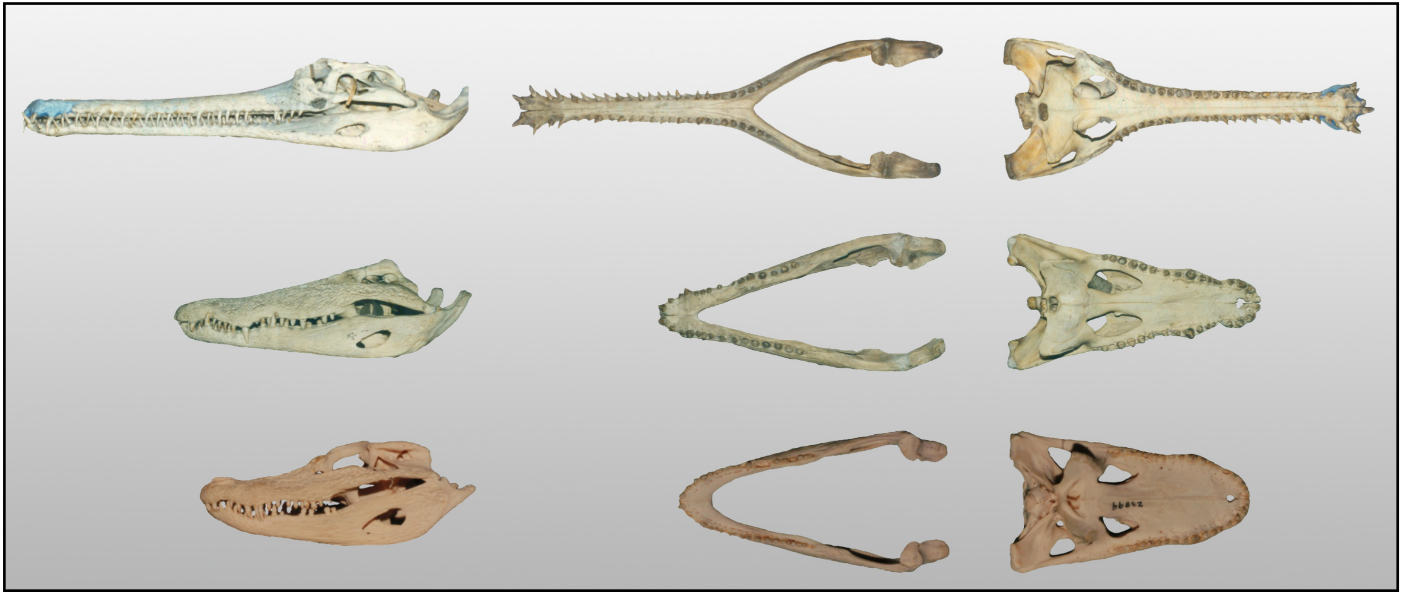


Fig. 14. Comparison of the snout and skull shapes of an extant gharial (above), an extant crocodile (middle), and an extant alligator (below); modified from Walmsley et al., 2013.

force. It is much more important that agile and slippery nourishment can be grasped and held with the snout at the right moment. The latter is accomplished with numerous small and sharp teeth.

Crocodylian teeth are attached in sockets or cavities in the jawbones. They are cone-shaped and can therefore withstand strain from all directions. This is very important for large crocodylians with broad snouts, for example the **black caiman**. It can feed on mammals as large as pigs and ungulates, prey that struggles not to be food. The high bite force, together with the large number of teeth, allows the crocodile to retain its prey and drag it along or drown it. Crocodylian jaws cannot carry out lateral or masticating movements, instead large pieces are simply swallowed. In order to snap off bite-sized chunks of larger prey, crocodylians roll themselves in the so-called 'death roll' along their longitudinal axis while holding the prey in their snout.

The food spectrum is not only influenced by habitat and shape of the snout but also by body size. For the 12.5 meter long and 8.4 tons heavy ***Purussaurus*** (→ **diorama, lab tables**) the daily food intake was on average approximately 40.6 kilograms. The extreme body size of this giant caiman most likely allowed it to feed not only on large fish and aquatic birds but also on giant turtles, rodents, sloths, and armadillos. Differences in diet are not only observable between species with different body sizes but also among size classes or developmental stages within a species. Young caimans for instance feed mainly on insects, molluscs, snails, and fish, whereas mature animals eat snakes, turtles, birds, and mammals. Analysis of gut contents from variously sized Nile crocodiles (and

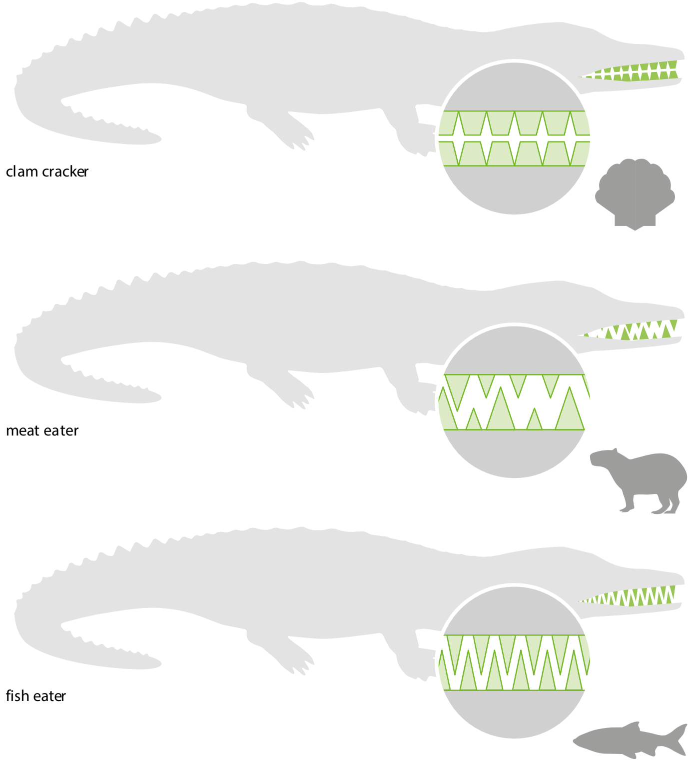


Fig. 15. Tooth shape typical for an animal feeding on hard-shelled prey items (above), a carnivorous animal hunting large prey (middle), and an animals preying mainly on fish (below); (illustration by Tara Gschwend, SIVIC UZH).

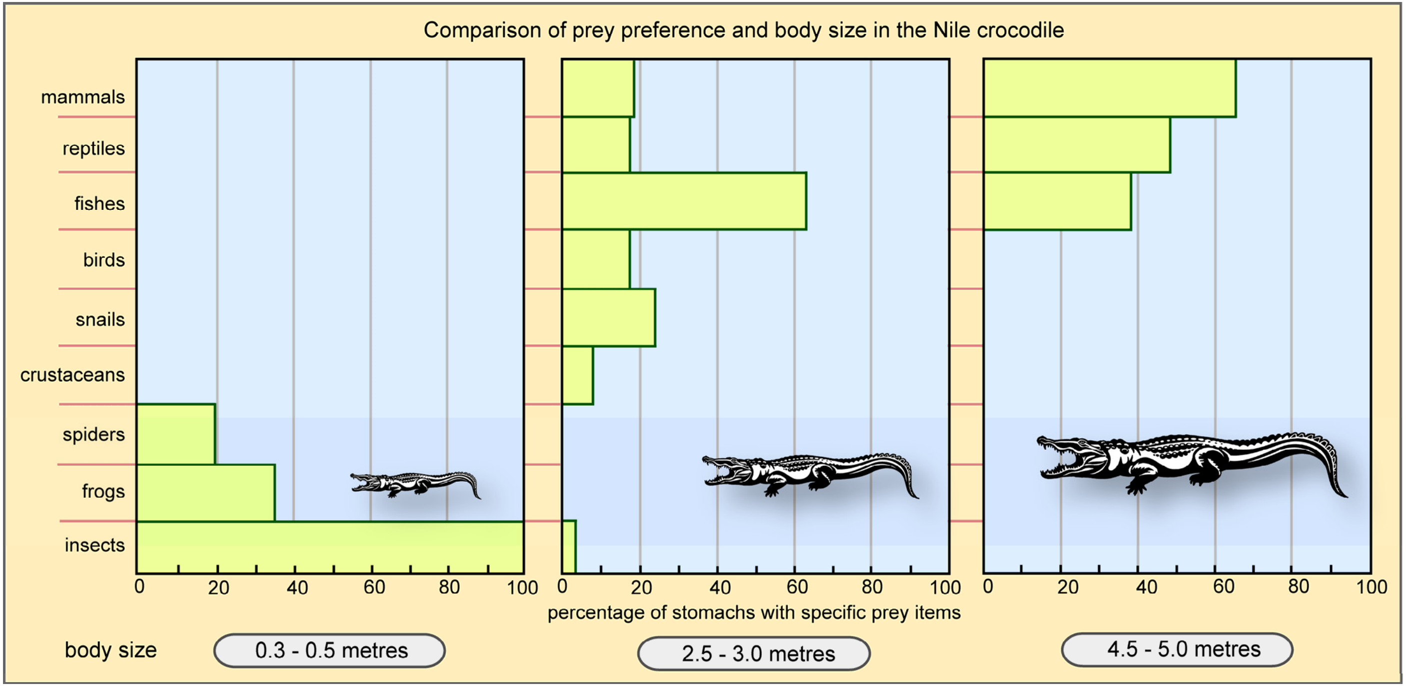


Fig. 16. Body size-dependent prey preference of the Nile crocodile *Crocodylus niloticus* (modified from Ross, 2002).

therefore various ages) serves as a further example, which is depicted in the following figure. The guts of all Nile crocodiles up to a body size of 0.5 meters contained insects, up to 40% of the latter also contained frogs and spiders. The gut contents of 60% of fully-grown and sexually mature animals contained mammals and 50% contained reptiles and fish but no smaller prey.

Fig. 17. *Purussaurus* and the giant rodent *Phoberomys* (illustration by Jorge Gonzalez, Argentina).

Breathing like birds

In crocodylians, as in birds, the air flows in one direction (through the lungs). This is in contrast to mammals, where the inhaled air reaches the finest branches for exchange of oxygen and carbon dioxide with the blood before taking the same way back during exhalation.

For air to be inhaled, the liver is pulled towards the posterior part of the body. This is achieved by contraction of a large muscle that is attached to the pubic bone of the pelvis and is connected to the surface of the liver by tendons. If the intercostal muscles are contracted at the same time, the volume of the chest is increased. This leads to a decrease in air pressure and causes air to enter the lungs. Exhaling either happens passively via relaxation of these muscles or actively via contraction of the abdominal muscles pushing the liver back into the front.

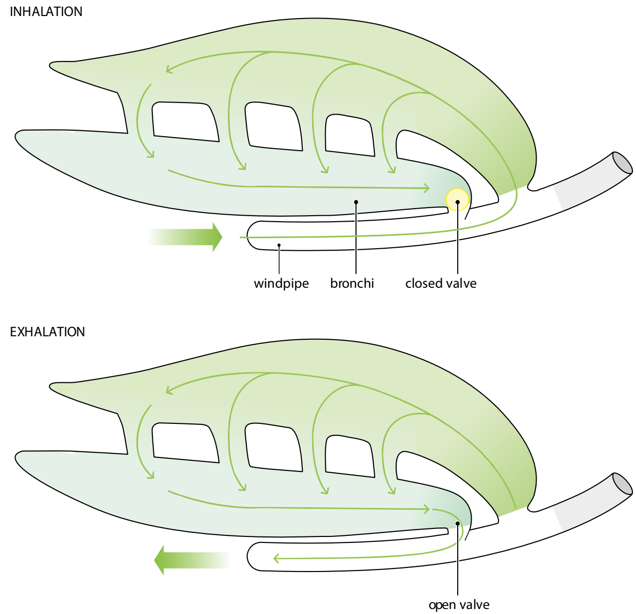


Fig. 18. Schematic drawing of the air ventilating the crocodylian lung during inhalation (above) and exhalation (below); redrawn and modified after Schachner et al., 2013 (illustration: Tara Gschwend; SIVIC UZH).

Diverse locomotion patterns in water and on land

Crocodylians are able to walk on the bottom of lakes and rivers, to paddle on the surface of the water or to float in water vertically. When swimming, crocodylians hold their forelimbs close to the body, while movements with the powerful tail propel them forward. The hind limbs hang loosely. Normally crocodylians reach a velocity of 2-4 km/h when swimming. They can accelerate up to 10 km/h when escaping danger or chasing prey. For comparison, the world record in crawling or butterfly stroke since 2009 is slightly over 7 km/h. With their strong tail, crocodylians are even able to spring vertically out of water.

On land, the crocodylian tail swipes over the ground. In the most common terrestrial locomotion type the extremities are rotated beneath the body horizontally, as in walking mammals. This way crocodylians are able to reach a velocity of 2-4km/h. The sprawling gait typical for lizards is used by crocodylians in order to move faster. On slippery surfaces such as mud, they slide on their bellies.

The gharial and some true crocodile species, usually smaller individuals, have been observed to gallop, in contrast to the alligator. This is linked to differences in leg and chest musculature. The hind limbs push the body forward and lift it from the ground, just like in horses. The forelimbs pick up the weight during touchdown and the hind limbs are pushed forward for the next cycle. The Johnston's or freshwater crocodile (*Crocodylus johnstoni*) can reach a maximum speed of around 18 km/h when galloping. This approximates the average velocity when cycling. However, this locomotion type can only be used for small distances of 15 to 20 meters, as it is energy consuming.

The anatomy of the crocodylian heart is unique. Unlike other reptiles, it is subdivided in four separate chambers, as in the case of birds and mammals. Snakes, lizards and turtles have a heart with only three chambers: two atria and one incompletely subdivided main chamber where oxygen-rich and oxygen -deficient blood meet. The main chamber in crocodylians, however, is subdivided into two chambers by a septum. In contrast to birds and mammals, they do have two aortae, a feature also present in other reptiles. Therefore, oxygen-deficient blood can be redirected into the systemic circulation instead of the pulmonary circulation if necessary. This happens particularly when diving, since the animal cannot breathe and the blood therefore is not enriched with oxygen. Additionally, the heartbeat is lowered from about

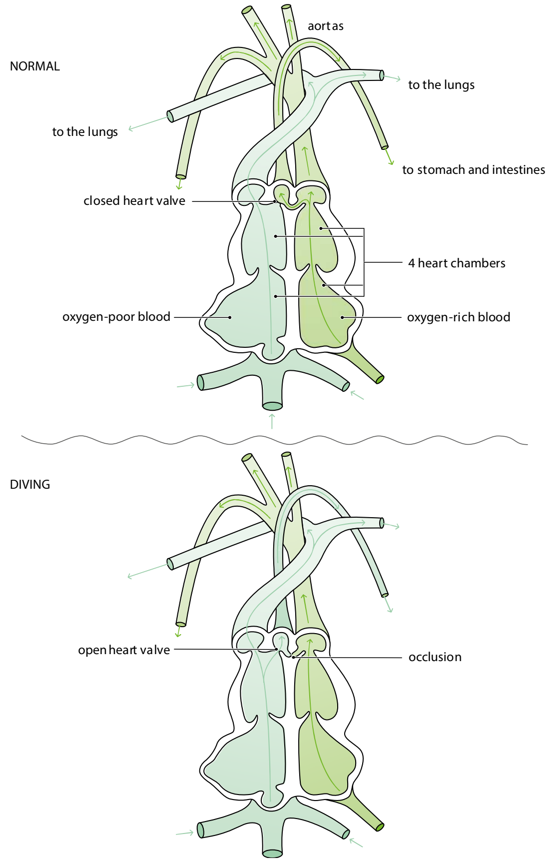


Fig. 19. Illustration on blood circulation on land and during diving (modified based on Richardson et al., 2002; illustration by Tara Gschwend; SIVIC UZH). During the diving period, oxygen-deficient blood can be redirected into the systemic instead of the pulmonary circulation.

Fig. 20. Juvenile of a saltwater or estuarine crocodile *Crocodylus porosus*, on which the scalation pattern on the head and the elevated external narial opening is well visible.

thirty to two beats per minute and the oxygen demand is reduced, which allows crocodylians to spend up to two hours underwater. However, voluntary diving normally does not last longer than 15 minutes.

Communicative reptiles – from hatching to mating

Besides communicating with gestures such as beating the head on water or via body odours (pheromones), crocodylians also communicate using a set of sounds. They share this ability with their closest relatives, the birds; however, they do not have a specialised organ for the production of such sounds. These are produced by air flowing into a narrow opening in the glottis. Muscles alter the shape of the glottis, generating different sounds. Those sounds produced by crocodylians are restricted to calls that differ among species. The calls are perceived with their hearing organs which lack the auricles characteristic of humans and other mammals and can be held above the water surface while swimming. Crocodylians can also communicate over low frequency acoustic waves generated under water; these are perceivable over long distances by conspecifics, but not by humans.

Vocal expression is already initiated in the egg; specific hatching-sounds synchronise hatching within a nest and signal the mother to open up the nest. Young animals have a diverse set of calls. The sounds before and during hatching serve to communicate with siblings or with the mother and are distinct from the ones produced later in life. In mature crocodylians, roaring and hissing are solely used in courtship behaviour, defending of territory, or protection of youngsters.

Scales and osteoderms serve for protection and thermoregulation

The outermost layer of the reptile skin contains keratinous scales of different size and shape. Crocodylian scales are flat and more or less square-shaped on the ventral side, therefore this area of the skin is often used in the leather industry. Roundish scales with an elevated middle part cover the flanks and the neck. Along the back, right underneath the scales, dermal bones called osteoderms are formed. They fulfil several functions. For one they form a shell protecting the internal organs against harm, and also contribute to the weight-bearing function of the dorsal spines ofvertebral column vertebrae. Osteoderms are also amply supplied with blood, which helps in thermoregulation, as increase or decrease in blood supply regulates heat exchange with the environment. The degree of ossification on the ventral side varies between species. The crocodylian tail is covered with scales that are hardened despite not containing bone tissue. These scales are protruding vertically from the tail, which greatly increases the surface area helping thermoregulation as well as swimming.

The colour of crocodylians is determined by pigment cells lying directly underneath the outer layer of skin. Small dark-brown or black pigment within the epidermis is either assembled in grains or dispersed forming ornament-like patterns. The exact colour of an individual is determined by genetic and environmental factors.

Fig. 21. Sun-bathing old individual of the saltwater or estuarine crocodile *Crocodylus porosus*. The 4 to 5 m long animal is opens its snout to prevent overheating of its head region.

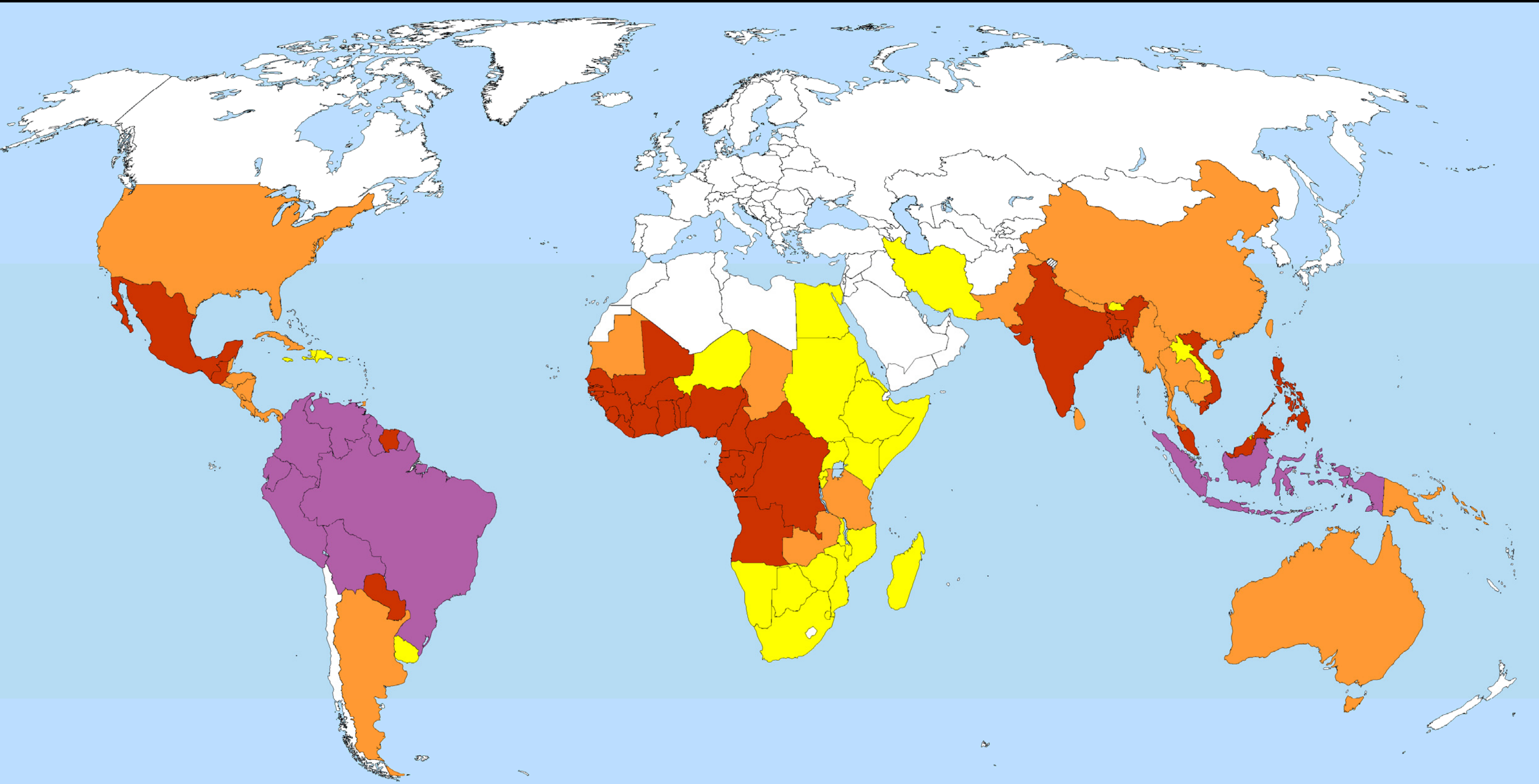
Half of all crocodylian species are endangered

The greatest threat to crocodylians is human-related. Around half of all crocodylian species are close to extinction because they are hunted for leather and meat, in addition to habitat and nest destruction.

In the wild, the eggs and young animals are subject to strong natural selection. An estimated 90% of crocodylians die within the first year due to predators, unfavourable environmental conditions or destruction of nests. Humans however, pose the greatest risk to crocodylians: we have changed their habitat, destroyed their nests and hunted more animals than are being killed by their natural predators.

Hunting was unrestricted during the fifties and sixties, during the late sixties and early seventies national and international laws were issued. Crocodylians are still hunted but the methods as well as the minimum size of animals that can be killed are usually restricted. Eggs that were found in the wild and sometimes even young animals are raised on crocodile farms. This helps to control the process of slaughter for meat production and collection of eggs may provide an incentive to preserve natural habitats of crocodylians. Despite all efforts for protection, almost half of the 23 extant crocodylian species are threatened with a high to very high risk of extinction in the near future.

Fig. 22. Map showing the number of crocodylian species worldwide (map: Rodolfo C. Ferioli in Britton, 1995-2012). Colour legend: purple, 4-6 species; red, 3 species; orange, 2 species, yellow, 1 species; white, no crocodylian record.



Inhabitants of the tropics and subtropics

The 23 extant crocodylian species are almost exclusively present in the tropics and subtropics. The **American alligator** (***Alligator mississippiensis***) and the **Chinese alligator** (***Alligator sinensis***) are the most cold-tolerant species and are thus the ones to inhabit rather northern areas. The seven alligator and caiman species (Alligatoridae) are mostly found in North-, Central- and South America. The Chinese alligator is the only exception; its distribution is limited to an area around the lower part of the Yangtze River in eastern China. The **Indian gharial** (***Gavialis gangeticus***) is distributed in certain areas in India as well as adjacent countries whereas the **false** or **Sunda gharial** (***Tomistoma schlegelii***) is found in very confined regions in Indonesia and Malaysia.

With a population size of over one million animals, the **spectacled caiman** (or common caiman, ***Caiman crocodilus***) and the **American alligator** have the highest numbers of wild individuals. Inhabiting 41 out of 54 African countries including Madagascar, the **Nile crocodile** (***Crocodylus niloticus***) has the most widespread geographical distribution.

Temperature-dependent sex determination and long lifespan

Crocodylians can reach an age of 70 years or more. Development starts in the egg and is largely driven by temperature within the nest. Sex determination depends on the temperature within the nest during the first 14 to 21 days after the egg was laid. Eggs that are subject to temperatures between 32 and 33°C become males, whereas temperatures below 31°C as well as higher than 33°C result in females. During the mating season, the timing of which varies between species and inhabited areas, females call attention to themselves using grunting or barking sounds. Males respond with loud roaring that besides being used to attract females, also serve for delimiting territory. Occasionally male fights for territory end with death of one competitor.

Crocodylians reproduce by laying eggs into self-built nests. Some are in the form of mounds of ripped-off plant material that is accumulated, so that bacterial decomposition creates a uniformly humid and warm environment. Another kind of nests consists of pits in the ground that are dug out with the legs and are covered with soil material or a mixture of soil and plant material. A clutch comprises of ten to one hundred eggs, varying with the size of the nest. Depending on the temperature within the nest, the eggs are incubated for two to three months; during this time, the female stays close to the nest in order to open it when the juveniles hatch.

Quick hunters in fresh- and brackish water

Crocodylians are amphibians and most species are bound to freshwater within either tropical rainforests or open, sunny areas. Only the **saltwater-** or **estuarine crocodyle** (***Crocodylus porosus***) lives almost exclusively in brackish water, occasionally also other *Crocodylus* species can be found there. In general, crocodylians prefer standing or quietly flowing waters, the smooth-fronted caiman and Cuvier's dwarf caiman (*Paleosuchus*) however, stay in rapidly flowing and turbulent rivers or streams occasionally. If two or more crocodylian species live together (sympatrically), they have different diets.

Crocodylians are carnivorous and feed on all animals they are able to catch during their rapid attacks. A considerable part of their nutrition may consist of plant material. Besides local populations of other animals, the constitution of their diet also depends on size of the prey as well as their own size. Crocodylians change their food habits during their lifetime, as they increase in body size they eat less invertebrates and feed on increasingly larger vertebrates instead. Molluscs, crabs and fish are a substantial part of the diet of an adult crocodylian. The preference for fish seems to correlate with length of the snout, as species with long snouts feed almost exclusively on fish.

Fig. 23. Small crocodile which just caught a toad.

OVERVIEW OF TAXA ON DISPLAY

1. Saltwater- or estuarine crocodile, *Crocodylus porosus* (extant) (→ **large lab table**)

As usual in true crocodiles, mandible and maxilla are similar in breadth and the teeth of the lower jaw are therefore visible when the mouth is closed. With a length of up to 7 meters, the estuarine crocodile is the larg-

est extant crocodylian, along with the Nile crocodile. Since the animals inhabit the islands and coastal areas of Southeast Asia and North Australia, they are also called saltwater crocodiles (or 'Salties').

Fig. 24-25. Estuarine crocodile skull in the exhibition. The teeth of the lower jaw are visible from the side when the snout is closed.

2. American alligator, *Alligator mississippiensis* (extant) (→ **large lab table**)

The American alligator is exclusively found in swamps, lakes and marshland in the Southeastern states of the USA. In contrast to crocodiles, the skulls of alligators and caimans are broader than their mandibles; therefore, the teeth of the lower jaw are covered by the upper jaw and are not visible on the sides when the mouth is closed. Alligators can reach a size of up to six meters and feed on a broad spectrum of prey, ranging from small invertebrates such as snails to fish, birds and reptiles.

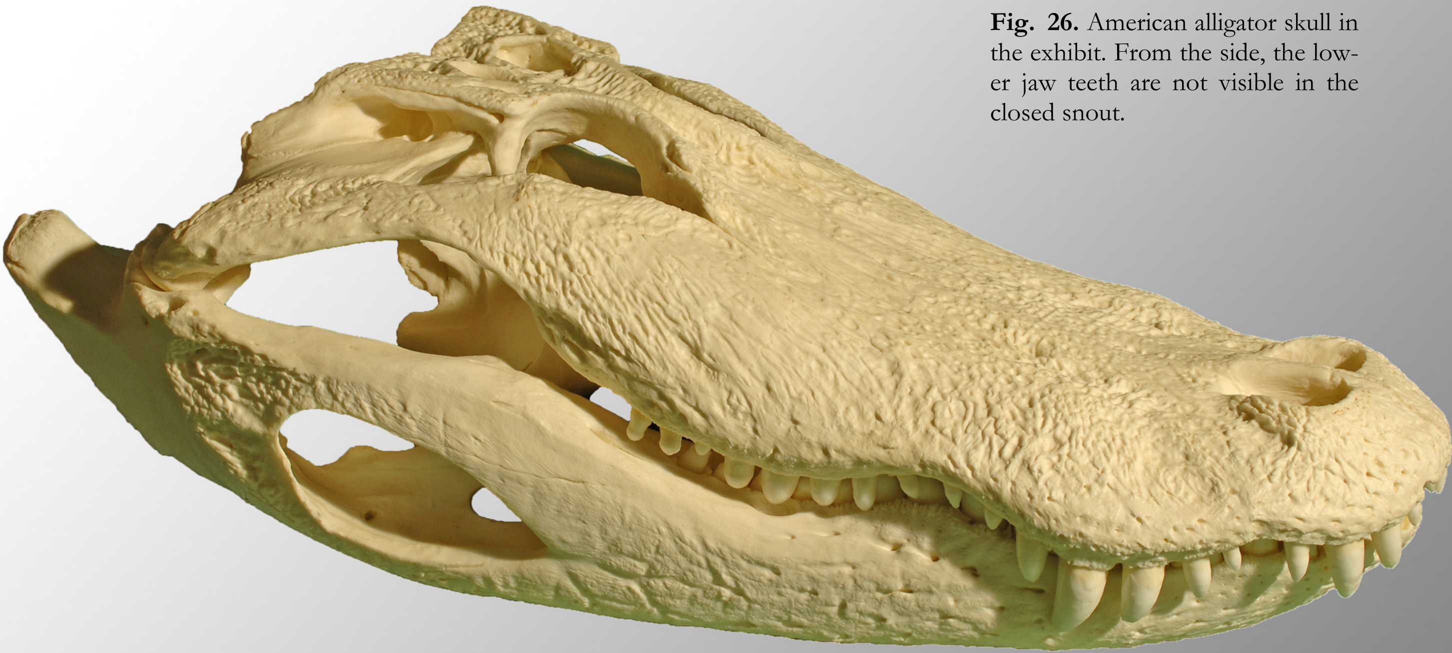


Fig. 26. American alligator skull in the exhibit. From the side, the lower jaw teeth are not visible in the closed snout.

3. Indian gharial *Gavialis gangeticus* (extant) (→ **large lab table**)

The distribution of the Indian gharial is limited to a few river courses in India and Nepal nowadays. Its paddle-like tail and the only poorly developed arms and legs indicate that the Indian gharial is well adapted to an aquatic lifestyle. The animals can be up to six meters in length. The long, slender snout does not offer much resistance in rapidly flowing water and the large number of teeth in its mouth make the Indian gharial a good fisher. In the year 2007, the species was listed as "*critically endangered*" by the International Union for Conservation of Nature (IUCN) since there were less than 200 animals in the wild.

Fig. 27. Indian gharial skull in the exhibition. The teeth of the lower and upper jaws are visible from the side when the snout is closed.

4. ***Purussaurus*** **(fossil)** (→ **lab tables, diorama**)

The caiman *Purussaurus* was the largest and heaviest fossil crocodylian from Urumaco and therefore the top predator within the river systems at its time. The skull is massive and even large prey could be caught effortlessly with the large teeth in the jaw. The diet of *Purussaurus* most likely consisted of small crocodylians, large turtles, fish and giant mammals such as the capybara-like rodent ***Phoberomys***, which weighed around 500 kg. Due to the absence of large carnivorous mammals in Urumaco, there was no competition for prey.

Fig. 28. The holotype skull (in top view; only the left jaw articulation is missing) of *Purussaurus mirandai* from the collection in Coro, Venezuela. Some bone sutures have been marked with white paint. The tip of the snout is to the right. The external narial opening is visible as a large central depression in the mid snout region.

Fig. 29. Naturally weathered and exposed accumulation of bones of a large *Purussaurus* specimen in the Badlands of Urumaco.

Fig. 30. Skeletal remains of another large specimen of *Purussaurus*, which has been collected during a PIMUZ-excursion for students, and which is since then deposited at the collections of the palaeontological museum at Urumaco. Student Olivier Strauss (as scale) described the postcranial bones in his Masters thesis.

Fig. 31. Images of the excavation site of the large *Purussaurus* specimen, collected in the Urumaco Badlands during the PIMUZ-excursion in fall 2013. **Left:** The bones are stabilised with glue and packed for transport. **Right:** In the foreground the giant lower jaw of the animal, as well as of bones are visible. Behind, from left to right: the Venezuelan palaeontologist and local Urumaco expert Rodolfo Sánchez, Torsten Scheyer, and Olivier Strauss.

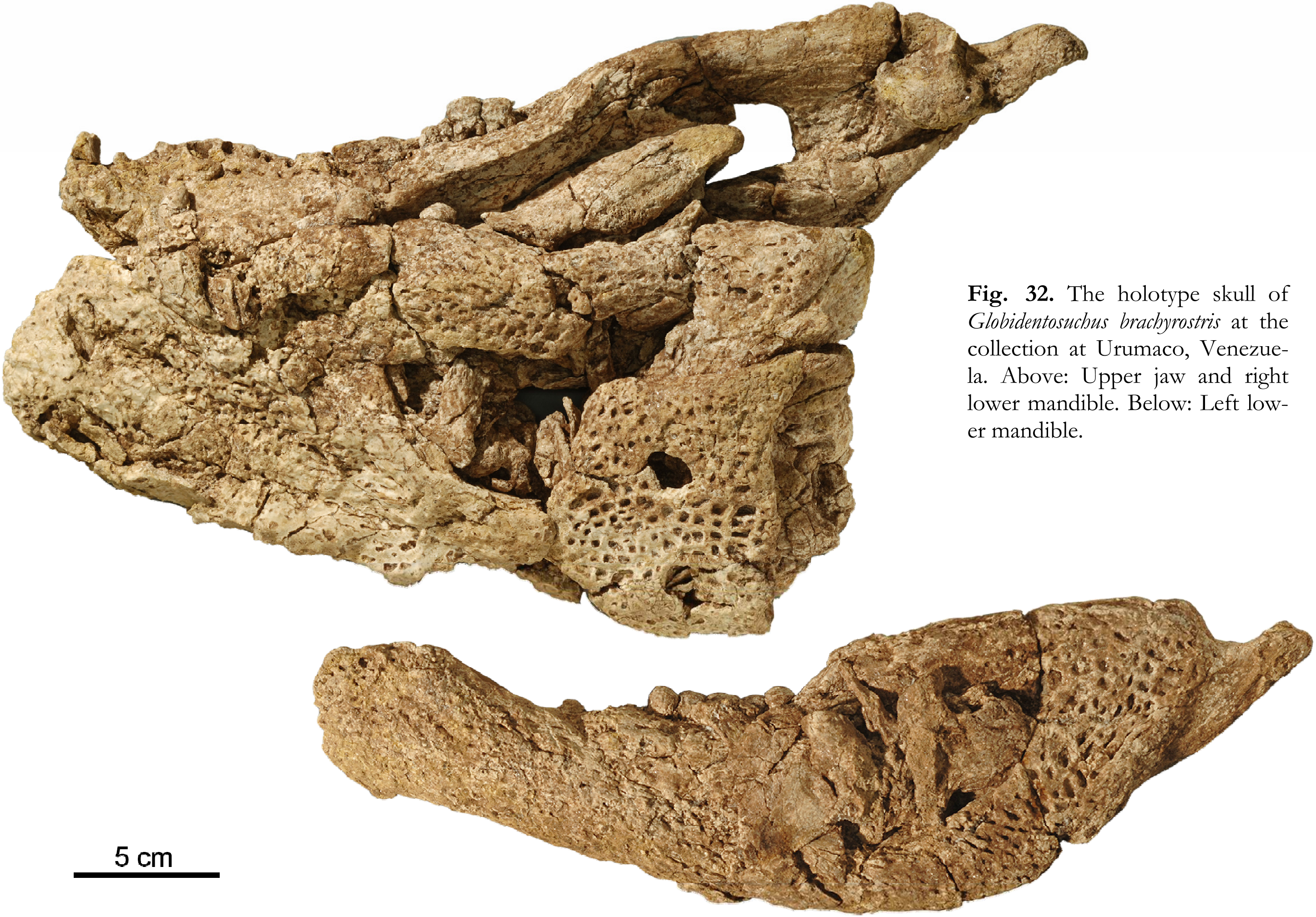


Fig. 32. The holotype skull of *Globidentosuchus brachyrostris* at the collection at Urumaco, Venezuela. Above: Upper jaw and right lower mandible. Below: Left lower mandible.

5. ***Globidentosuchus*** **(fossil)** (→ **large lab table, diorama**)

Globidentosuchus brachyrostris was a small, basal representative of caimans uniting many ancestral characteristics of its clade. The rear part of its powerful jaw was densely lined with button-like teeth that were used for cracking open muscles or snails.

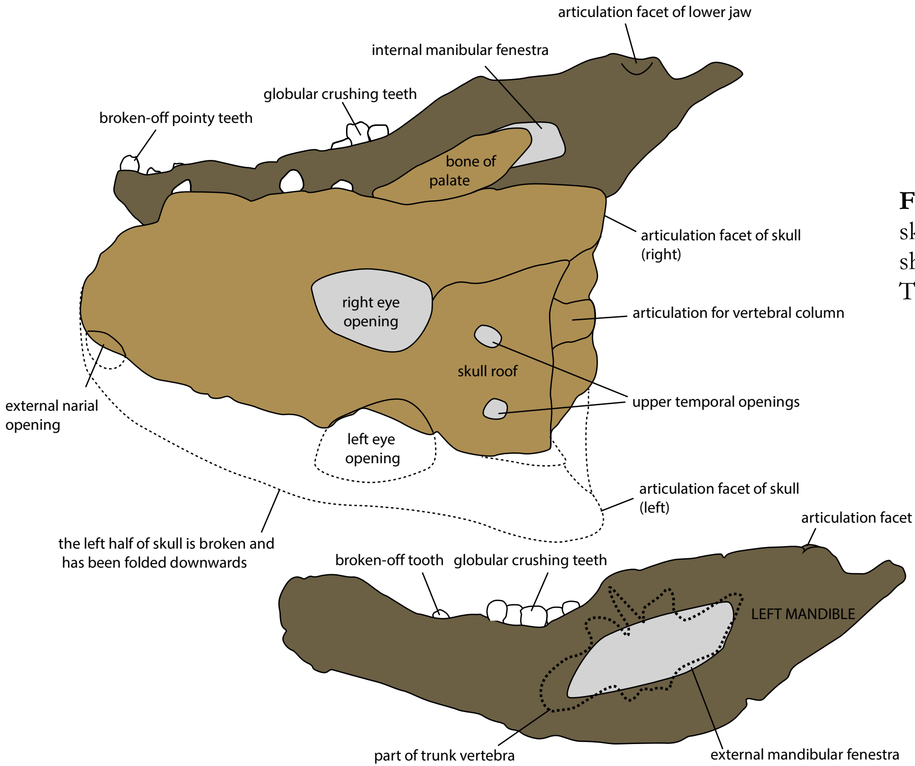


Fig. 33. Interpretational sketch of the bones shown in Fig. 32 (by Torsten Scheyer).

6. ***Mourasuchus*** **(fossil) (→ large lab table, diorama)**

Mourasuchus is characterised as being "duck-like",due to its flat, protruding snout. There was a large number of small, morphologically similar teeth on the weakly distinct jaw, which was only poorly adapted for catching larger prey. *Mourasuchus* therefore likely fed on small, sluggish prey such as small fish or crustaceans.

Fig. 34. The holotype skull, the right lower mandible and a scapula of *Mourasuchus arendsi* in the collection at Coro, Venezuela.

Fig. 35. Life reconstruction of *Mourasuchus* (Illustration: Jorge Gonzalez, Argentina).

7. *Gryposuchus* (fossil) (→ **small lab table, diorama**)
Gryposuchus croizati had a long and relatively slender snout spiked with a large number of sharp teeth similar to the extant **Indian gharial** (*Gavialis gangeticus*). The morphology of the snout was ideal for a carnivore and it did not offer much resistance in rapidly flowing water. This extinct species reached up to ten meters in length and was therefore the largest gharial recorded to date.

8. *Ticinosuchus ferox* (fossil) (→ **"tree of life"**)
Ticinosuchus ferox lived approximately 242 Million years ago and was found in an area of what is today the Swiss canton Ticino. It was at the time the top predator in the food chain within terrestrial ecosystems. In contrast to crocodylians, *Ticinosuchus* had a high and comparably gracile skull with five large openings on each side and flat teeth that were bent towards the rear. Its skull had a similar appearance to that of carnivorous dinosaurs such as *Tyrannosaurus rex*. The original fossil based on which the species was described for the first time can be found in the **permanent exhibition** of the Palaeontological Museum (PIMUZ).

Fig. 36. The skull (paratype) of *Gryposuchus croizati* in the Urumaco collections, together with an expert on fossil crocodylians, Dr. Massimo Delfino from the University of Torino, Italy.

9. *Sarcosuchus* (fossil) (→ **"crocodylian tree"**)

The largest known representative of the Crocodylomorpha so far is *Sarcosuchus imperator*, with up to 12 meters in length and a weight of up to 8 t. This impressive animal is known from the Cretaceous of Niger in West Africa. The extremely broad nostril at the tip of the long and slender snout is one of its striking features. The adults most likely fed on a broad spectrum of prey, which included even large dinosaurs.

Fig. 37-38. The skull *Sarcosuchus* in the exhibition, in angled side and frontal view.

10. *Metriorhynchus* (fossil) (→ **large lab table**)

Metriorhynchus superciliosus belonged to a group of marine crocodylians called Thalattosuchia. They had a streamlined body, their arms and legs were in the form of paddles and they had a caudal fin. They were widely distributed in the epicontinental shallow seas of the Middle and Upper Jurassic. With its long and slender snout, *Metriorhynchus* hunted molluscs, such as belemnites, and fish.

11. *Diplocynodon* (fossil)
The alligator *Diplocynodon* was one of the most abundant European crocodylians during the Palaeogene and the Neogene (49 to 11 million years ago). Some of the best-preserved finds are from the World Heritage natural site of Messel close to Darmstadt (Hessen, Germany) - it sometimes is referred to as the "Messel-crocodile". This Lagerstätte became famous for findings of dog-sized fossil horses within the 47 million years old oil shale layers of the lake of Maar in Messel (Eocene). The appearance of the small to middle-sized *Diplocynodon* was similar to extant alligators. They had osteoderms on the neck, the back, the abdomen and the tail. An original find of *Diplocynodon*, the holotype of "*Dipocynodon buetikonensis"* which was described by the German palaeontologist Hermann von Meyer in 1855, is displayed in the **permanent exhibition** of the Palaeontological Museum. The skull with remains of the mandible was found in the upper freshwater molasses (Miocene) of the Lindenberg in Büttikon in Canton Aargau. The original fossil can be found in the **permanent exhibition** of the **Palaeontological** Museum.

Fig. 39. The skull of *Metriorhynchus superciliosus* from the PIMUZ-collections in top view (above) and side view below).

Fig. 40. The holotype skull and associated bones of *Diplocynodon buetikonensis* at the Palaeontological Museum (PIMUZ).

There are different objects and reconstructions of extant and fossil crocodylians displayed in the exhibition. Some of them were created specifically for the exhibition "Das Krokodil im Baum". Others, such as the skull of the extant saltwater crocodiles, the Indian gharial or the American alligator were produced by the company BoneClones©, which produces casts of real bones and skulls. Since the objects displayed in the exhibition can be touched by the visitors, no real bones, but excellent replicas are displayed for hygienic and safety reasons.

Ticinosuchus – the hunter from Ticino

The holotype of *Ticinosuchus ferox*, the Middle Triassic hunter from Monte San Giorgio in Tessin is one of the most valuable fossils in the Palaeontological Museum. The real plate containing the almost complete, articulated fossil (**permanent exhibition**) according to which the species was described for the first time, was used as a model for the live reconstruction by Beat Scheffold at the entrance of the special exhibition. The original of this live reconstruction is displayed in the Museo dei Fosili di Meride in Ticino. Its surface was scanned with a surface scanner and reconstructed on the computer. The steps of this process were the following:

1. The surface of the original for the live reconstruction of *Ticinosuchus* was scanned in several steps using an ARTEC 3D-surface scanner. Similar to a regular camera, the scanner emits light impulses onto the object; several film cameras on the scanner absorb the reflection of these. In this way, an image of the object is produced systematically.
2. The scanned parts were merged into a complete model on the computer and are tested for mistakes or missing parts. The shape of the object is now represented as a mesh consisting of many polygons and triangles.
3. The model was cut virtually on the computer of Inspire AG in St. Gallen, a Spin-off of ETH Zurich, and prepared for 3D printing.
4. The different 'building blocks' were produced with 'Laser Sintering' technique. Here, a very fine synthetic material is melted using a laser

and thus deposited layer by layer on the model – the individual building blocks are 'growing' within the machine.

5. The finished 'building blocks' were cleaned and afterwards assembled and glued together. In order to reduce the amount of material used and therefore the weight of the model, the object is hollow on the inside, similar to a chocolate Easter rabbit.
6. In a last step, the complete model was carefully ground and lacquered.

Objects on the lab tables

Some of the bones and skull fragments are not real bones or fossils but casts produced either in Venezuela or in Zurich at the PIMUZ. For most of them, a silicon mould was made in several layers. After removal of the original bone, a detailed negative image of the fossil remains within the silicon mould and can be filled with cast material. Here, a two component artificial resin was used instead of plaster, since the former is both lighter as well as less delicate. In the following, three cases are explained in more detail:

Fig. 41. Left: Images of the laser-sintered plastic parts of the life reconstruction of *Ticinosuchus* model parts at Inspire AG in St. Gallen. **Right:** Computer models of the right lower jaw and the upper jaw, as well as the still un-painted 3D plastic parts, of *Globidentosuchus*; produced at ANKA at KIT Karlsruhe, Germany,


Forschung & Entwicklung
Materialien und Prozesse

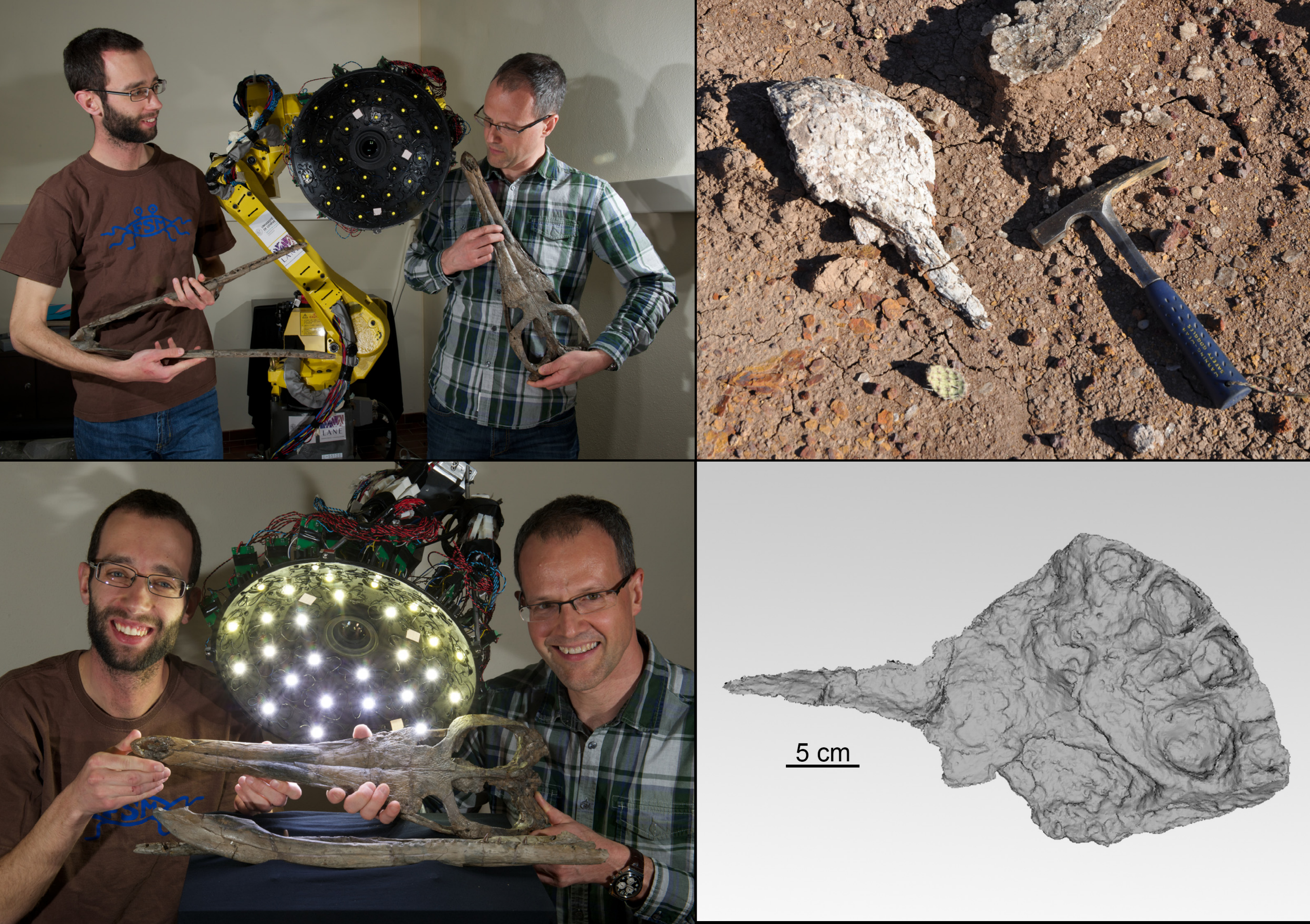
Globidentosuchus brachyrostris
(skull and mandible)

The skull and lower jaw of *Globidentosuchus brachyrostris* from the upper Miocene from Venezuela were scanned using computed tomography (CT). For the production of a detailed cast of the fossil, the shape and exterior structures were important but not the inner bone structure. In the scan, the robust mandible and the spherical cracking teeth in the posterior part of the jaw are well visible. The scan data were sent to ANKA in Karlsruhe where they were virtually cut and prepared for printing. In contrast to *Ticinosuchus,* a 3D printer was used in which a molten synthetic material is deposited on the model layer by layer with a delicate nozzle. A copy of the fossil is now exhibited as a three dimensional print without an interior cavity. After gluing together, the individual parts were cleaned and painted.

Metriorhynchus superciliosus
(skull and mandible)

The skull and mandible of this marine crocodylian was scanned at the University of Geneva in the laboratory of Prof. Michel Milinkovitch (Department of Genetics and Evolution; www.lanevol.org). A robot equipped with many high-performance-LEDs and a digital camera was used. The mobile arm of the robot makes it possible for the fossils to be photographed from all sides in a short time. The LEDs illuminate the fossil objects optimally at different angles. Using a photogrammetry software, the three dimensional, virtual model of the bones can be digitally created. As for *Ticinosuchus*, the printing was conducted at INSPIRE AG in St. Gallen.

Fig. 42. Left: Images of the scanning robot arm at the Lanevol-Lab of Prof. Milinkovitch (right side in photo). The scanning process was supervised by Lanevol student Antonio Martins. **Right:** Image of the place of finding of the premaxilla (in top view) of *Purussaurus* in the Miocene Badlands of Urumaco, followed by the resulting computer model (internal view with tooth sockets)


5 cm

Purussaurus mirandai
(tip of snout)

The isolated premaxilla, the foremost tip of the snout, of a large but weathered skull of *Purussaurus mirandai* was discovered in the fall of 2013 during a student fieldwork excursion in Urumaco, Venezuela. Instead of conventional silicon casts, the bone was scanned from all sides using ARTEC 3D-suface scanner. The resulting computer model was also printed using the 'Laser Sintering' procedure at INSPIRE AG in St. Gallen.

The live reconstruction of the Venezuelan crocodylians from the upper Miocene

The caiman *Globidentosuchus*, the huge *Purussaurus, Mourasuchus,* and the gharial *Gryposuchus* were produced after drawing templates, plaster casts and photographs of the original bones from Venezuela by the scientific illustrator and model builder Beat Scheffold, staff member at the Palaeontological Institute and Museum. First, the proportions of the original bones were measured and transferred into a plastic- and styrofoam form. Afterwards, the muscles and the skin as well as the surface structures were modelled onto these basic forms using synthetic resin and artificial eyeballs made of glass were inserted. Comparison to extant crocodylians is important for all these steps. This results in impressive, natural-looking live reconstructions of the extinct animals, which largely exceeded the maximum size of extant forms.

Fig. 43. 'Developmental series' of the life reconstruction models of *Globidentosuchus* (→ diorama), built by Beat Scheffold, PIMUZ.

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Fig. 44. 'Developmental series' of the life reconstruction models of *Purussaurus* (→ diorama), built by Beat Scheffold, PIMUZ.

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ACKNOWLEDGEMENTS

To the teams of the Palaeontological Institute & Museum and the Zoological Museum, UZH.

Dr. Ingmar Werneburg, Scidinge Hall Verlag

We thank Gabriel Aguirre-Fernández, Robert J. Asher, and Ashley Latimer for suggestions to improve the text.

Concept, scenography, & execution of the exhibition
fischteich, Peter Kuntner, & Stephan Lichtensteiger, Aarau; Isabel Klusman, Life Science Zurich, UZH & ETH

Exponate
Christian Klug, Marcelo Sánchez, Beat Scheffold, Torsten Scheyer, Daniela Abegg, & Fiona Straehl, Palaeontological Institute & Museum , UZH; Marianne Haffner, Beat Häusler, Barbara Oberholzer, & Janine Mazenauer, Zoological Museum, UZH; Jürgen Nauber & Maria Schönbächler, ETH Zurich; Dr. Lindsay Zanno and colleagues, North Carolina Museum of Natural Sciences, Raleigh, NC, USA; Prof. John Hutchinson, Royal Veterinary College, London, UK

3D printing
Prof. Dr. Michel Milinkovitch and the LANEVOL-laboratory, University Geneva, Switzerland; Dr. Thomas van de Kamp, Michael Drees, and colleagues, ANKA Synchrotron Facility, Karlsruher Institut für Technologie, Germany; Raphael Schmid and colleagues, INSPIRE AG, St. Gallen, Switzerland

Financing
Swiss National Science Foundation „Agora – Taking research to the public“ (Funding No. CRAGP3_151505 / 1); Marcelo Sánchez, Palaeontological Institute & Museum , UZH; Life Science Zurich, UZH & ETH; Faculty of Science UZH

Image credits:
Torsten Scheyer (PIMUZ, Zurich): Figs. 2-3, 5 (photo), 6, 24 -29, 31-40, 41 (right bottom)
Beat Scheffold (PIMUZ, Zurich): Figs. 4, 43-44
Elke Goldbeck (Zurich): Fig. 23
Raffael Schmid (INSPIRE AG, St. Gallen): Fig. 41 (left)
Adrien Debry (LANEVOL, Geneva): Fig. 42 (left)
Christian Klug (PIMUZ, Zurich): Figs. 20-21

Original German version available: *Das Krokodil im Baum - Eine Ausstellung über Evolution und Biodiversität* (ISBN: 978-3-905923-19-3)
English translation by: Anita Schweizer (PIMUZ, Zurich)

This broschure was made for the special exhibition „Das Krokodil im Baum / Crocodile in a tree“ of the Palaeontological Institute and Museums of the University of Zurich and Life Science Zurich (UZH & ETH), from September 29th, 2015, until January 31st, 2016.

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zoologisches museum der Universität Zürich
Universität Zürich UZH
ETH Zürich
life science zurich
FNSNF Swiss National Science Foundation